

THE EFFECTS OF GRAZING AND SITE PRODUCTIVITY ON CARABID
BEETLES (COLEOPTERA: CARABIDAE) IN A SEMI-ARID GRASSLAND

By

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ABSTRACT

The grasslands of British Columbia (BC), Canada are an important resource for the ranching industry, even though they occupy less than one percent of BC's land area. Cattle grazing can alter the structure and composition of the plant community, which may indirectly affect insect communities. Insects are an integral component of grassland ecosystems; for example, carabid beetles (Coleoptera: Carabidae) prey on lower trophic levels while providing food resources for upper trophic levels. In the semi-arid grasslands of southern BC, soil-water availability increases with elevation, and plant community composition differs along the elevation (productivity) gradient. I investigated the effects of cattle grazing and productivity on ground beetle abundance, dried weight (biomass), species richness and diversity. Over three sessions of pitfall trapping in 2008 in Lac Du Bois BC Provincial Park, 600 individuals of six carabid species were captured. To test for main and interacting effects of elevation, grazing, and month of capture, carabid beetles were quantified by trap for abundance, dried weight (biomass), species richness and Shannon's diversity. I found that elevation was the most important predictor of carabid abundance, biomass, species richness and diversity. Lower elevation had an average abundance of 1.04 carabids, dried weight of 25.50 mg, species richness of 0.46 and Shannon diversity of 0.06, compared to upper elevation with an average abundance of 2.88 carabids, dried weight of 113.71 mg, species richness of 1.00 and Shannon diversity of 0.15. Grazing had a significant effect on carabid diversity with higher diversity in upper elevations. There were significant effects of month of capture on carabid beetle biomass, species richness, and Shannon diversity. To examine energy differences, calorimetry experiments were performed on the seeds of four dominant grasses (*Poa sandbergii*, *Pseudoroegneria spicata*, *Festuca campestris*, and *Poa pratensis*) and on four carabid beetles (*Carabus taedatus*, *Calosoma moniliatum*, *Amara obesa*, and *Cymindis borealis*). Average calories per gram were significantly different between two dominant species of carabid, *Cymindis borealis* (3114.741 cal/g), and *Carabus taedatus* (5321.862 cal/g). Grass species did not differ in calories per gram of seed. Caloric value (calories per gram x gram) of carabids and seeds were higher in the upper grasslands compared to the lower grasslands. As one of three Provincial parks that protect natural grasslands, the management of Lac Du Bois benefits by considering biodiversity of all biota, including invertebrates.

keywords: Carabidae, grassland, caloric value, cattle grazing, productivity.

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CHAPTER 1

Introduction

Biodiversity in grasslands is declining due to habitat loss, non-native invasive species and over-grazing (Aguair 2005). Grassland conservation and management requires an understanding of the effects of disturbance caused by over-grazing on biodiversity. Species of limited mobility, such as wingless insects (e.g., most ground beetles (Coleoptera:Carabidae)), face the greatest risk due to their reduced ability for successful migration (Malcom and Markham 2000). It is important to promote grassland diversity through conservation of habitat and good management for native and endemic plants and animals.

The grasslands of British Columbia (BC), Canada are widely used for cattle grazing, and only cover 0.8% of the provincial land base (GCC 2004). As of January 2009, BC runs five hundred and fifty-five thousand head of cattle (Statistics Canada 2009). Large herbivore grazing can change the structure of the plant community due to soil compaction, and the mechanical selection and removal of biomass (Holland and Detling 1990; Fleischner 1994; Rietkerk et al. 2000). Cattle grazing reduces biomass, creating spatial heterogeneity, and can increase plant species richness (Pykälä 2004; Dorrough et al. 2007). Management can optimize herbaceous plant species diversity; in grassland areas of BC, grazing tolerant plants dominate large swards that have experienced a long history of grazing and in these cases species diversity remains high with light or intermediate grazing pressure relative to no grazing or high grazing (Milchunas et al. 1988).

In semi-arid grasslands of the southern interior of BC, the water-limited landscapes experience a precipitation gradient: more rainfall occurs at higher elevations due to rainshadow effects (van Ryswyk et al. 1966). Different plant communities occur along these elevation gradients, with higher elevation grasslands producing more biomass than lower elevation grasslands (van Ryswyk et al. 1966). With higher levels of productivity, a few superior plant competitors dominate the community and thus plant species richness is

reduced (Kondoh et al. 2000). Vegetation structure and diversity can influence insect community structure. For example, Brose (2003) found that in wetlands, spatial heterogeneity of plants was an important predictor of carabid beetle species diversity.

There are many grassland invertebrate species. Selecting one group of invertebrates can be useful as a surrogate to predict changes in other invertebrate taxa (Rohr et al. 2007). One group in particular, ground beetles, also known as carabid beetles, (Coleoptera: Carabidae) are commonly monitored along environmental gradients (Weller and Ganzhorn 2004; Vanbergen et al. 2005; Suominen et al. 2008; Wenninger and Inouye 2008), used to rank environmental quality or severity of disturbance (Eyre et al. 1996; Phillips et al. 2006) and measured to quantify energy value (Zygmunt et al. 2006). Carabid beetles are predominantly an epigeal family, usually with reduced or absent wings. Carabids are sensitive to disturbance, and are usually polyphagous. My study focused on the effect of grazing at different levels of productivity along an elevation gradient on carabid abundance, biomass, diversity, and energy value.

AIMS AND STRUCTURE

My thesis examines the effect of grazing and productivity on the abundance, diversity, and biomass of carabid beetles in a grassland ecosystem. Furthermore, it examines the differences in energy value of carabid species and dominant grass seeds. I have organized the thesis into the following chapters:

Chapter 1: Introduction, Aims and Structure. This chapter introduces the topics and ideas examined throughout the rest of the thesis.

Chapter 2: Interacting Effects of Productivity, Grazing, and Month on Grassland Carabid Beetles. This chapter describes the vegetation communities at three elevation levels, and the carabid assemblages that inhabit them. The abundance, dried weight, species richness, and diversity of carabids are analyzed for differences by elevation, month of capture, and grazing.

The following research questions are examined:

1. Is the abundance, dried weight, species richness and diversity of carabid beetles affected by grassland site productivity (based on changes along an elevation gradient)?
2. Is the abundance, dried weight, species richness and diversity of carabid beetles affected by cattle grazing?
3. Is there a difference in the abundance, dried weight, species richness, and diversity of carabids with month of capture?

Chapter 3. The Energy Values of Carabid Beetles and Grass Seeds. In this chapter, I used a process called oxygen bomb calorimetry to compare the calories per gram and caloric value of four carabid beetle species, and of seeds of dominant grasses. I also examined the caloric values of carabids and seeds by elevation.

The following research questions are examined in this chapter:

1. Do *Cymindis borealis*, *Amara obesa*, *Calosoma moniliatum*, and *Carabus taedatus* differ in calories per gram? Does the caloric value of all individuals differ among species?
2. Do seeds of the two dominant grass species of the lower (*Poa sandbergii*, *Pseudorogenaria spicata*) and upper (*Festuca campestris*, *Poa pratensis*) grasslands differ in caloric value per gram? Does the caloric value of all inflorescences differ among species?
3. Does the caloric value of carabids and seeds change along a gradient of elevation?

Chapter 4. Synthesis and Implications for Management. This chapter summarizes results, outlines future directions for research, and discusses management implications of this research.

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CHAPTER 2

Interacting Effects of Productivity and Grazing on Grassland Carabid Beetles

INTRODUCTION

Half of the world's terrestrial land base is grazed by domesticated livestock (Havstad 2008). As a disturbance, grazing by large herbivores has direct effects on vegetation, such as selective mechanical removal of aboveground biomass, trampling of plants, and compaction of soil (Holland and Detling 1990; Rietkerk et al. 2000). Grassland community structure and function is consequently changed by cattle grazing (Holland and Detling 1990; Fleischner 1994). Plant diversity has been shown to decrease when there is a long history of large herbivore grazing (Milchunas et al. 1988), but intermediate levels of grazing can increase plant diversity (Grime 1973; Connell 1978), especially in areas of high site productivity (Osem et al. 2002; 2004).

Understanding patterns of grassland biodiversity is important because biodiversity can contribute to maintaining ecosystem function and economic value (West 1993; Kennedy et al. 2002). There is a good understanding of the impacts of grazing on plant communities, but little is known about grazing effects on grassland invertebrates or how site productivity might alter invertebrate diversity. One study showed that when plant diversity was low, as in areas of high site productivity, there was high insect diversity (Patrick et al. 2008); in other words, site productivity was positively correlated with insect diversity. In contrast, Haddad et al. (2001) found that areas of high site productivity and low plant diversity had low insect diversity, and areas of low site productivity and high plant diversity had high insect diversity. Patrick et al. (2008) measured the epigeal community through pitfall traps whereas Haddad et al. (2001) investigated above-ground insects with sweep nets, and this may account for some of the different results. However, Crisp et al. (1998) conducted a case study in New Zealand in which the proportion and diversity of native vegetation had a positive trend with native epigeal beetle diversity. Since there is a lack of consensus on how epigeal invertebrate

diversity varies along a productivity gradient, I examined the abundance, biomass, species richness, and Shannon diversity of carabid beetles along a grassland productivity gradient with and without cattle grazing.

Carabid beetles (Coleoptera: Carabidae) are a well-studied group that are often described as sensitive to disturbance and can therefore be used as bioindicators (Rainio and Niemelä 2003), or to rank environmental quality (Eyre et al. 1996). When studied as bioindicators, carabid populations are monitored to research the ecosystem health or even to measure accumulation of industrial heavy metals (Zygmunt et al. 2006). Carabid beetles serve an important role in grassland ecosystems; for example, carabids provide a food source for mammals, amphibians, birds and insects. If cattle alter the structure and composition of the grassland plant community, how might this affect insect diversity and composition?

According to Brose (2003), greater vegetation structure, as measured by height and layering, leads to an increase in insect diversity. Similarly, Kruess and Tschardtke (2002) and Patrick et al. (2008) have shown that higher vegetative productivity can result in a more diverse invertebrate community. Insects are sensitive to vegetation changes due to their requirements for oviposition sites, microsite preferences, hunting methods, and protection from predation (Eyre et al. 1996; Pöyry et al. 2006). Therefore, grazing and site productivity should influence insect diversity, at least indirectly, through plant community alteration.

Macroarthropod communities can be measurably changed by alterations to the plant community. Invertebrate communities may have reduced (Cagnolo et al. 2002), or increased (Siemann 1998) abundance and diversity with grazing. The study by Grandchamp et al. (2005) found that the management of grazing intensity in Swiss montane meadows was positively correlated with carabid abundance. Pöyry et al. (2006) found that insect species richness tends to decrease with grazing. Bottom-up effects can control arthropod herbivores and predators, for example, when plant biomass is removed through grazing, arthropod herbivore and predator abundances may decrease (Siemann 1998).

In British Columbia (BC), Canada, most of the natural grasslands are utilized for cattle grazing. Grassland management in BC therefore requires an understanding of how livestock affects grassland function. This study allowed me to test the following hypotheses:

1. The abundance, biomass, species richness and diversity of carabid beetles will be affected by grassland site productivity (based on changes along an elevation gradient). I predicted that carabid beetles will increase in abundance, biomass, species richness and diversity with site productivity.
2. The abundance, dried weight, species richness and diversity of carabid beetles will be affected by cattle grazing. I predict that cattle grazing will alter the structure and composition of the plant community, which, in turn, will reduce the abundance, biomass, species richness and diversity of carabid beetles. However, this effect will not be as strong at high productivity (elevation) sites compared to low productivity sites. In other words, there will be interacting effects on the beetle community between grazing and site productivity.
3. There will be no difference in the abundance, dried weight, species richness, and diversity of carabids with month of capture.

METHODS

Study Area

The grasslands of Lac Du Bois Provincial Park are located northwest of Kamloops in south central British Columbia, Canada. The park is a multi-use semi-arid grassland managed for cattle, recreation, and wildlife. The grasslands change in elevation over a short distance – from 350 m a.s.l. to 1100 m a.s.l. within ~ 10 km. Precipitation ranges from 250 mm/year at lower elevations to 350 mm/year at upper elevations, establishing a gradient of plant productivity (van Ryswyk et al. 1966). The study sites at upper elevations have a soil organic carbon content of ~ 150 g/2 dm³ and are dominated by rough fescue (*Festuca campestris* Rydb.) and Kentucky bluegrass (*Poa pratensis* L.). The study sites at lower elevations have a soil organic carbon content of approximately 40 g/2 dm³ and are dominated by big sagebrush (*Artemisia tridentata* Nutt.) and bluebunch wheatgrass (*Pseudorogeneria spicata* (Pursh) A. Löve) (van Ryswyk et al. 1966).

As well as experiencing disturbance from wildlife and recreation, the grassland is grazed by cattle from April to November, with some pastures grazed every other year. Several fenced cattle exclosures exist within the park to measure changes in vegetation with the exclusion of cattle grazing. Three of these exclosures were used in my experiment as “non-grazed” sites (Table 2.1). In May of 2008, I sampled eight field sites (four lower, four upper) and in July of 2008, two middle elevation grazed sites were added (Figure 2.1).

Table 2.1 Specific site information of cattle exclosures used as ungrazed sites (Rankin, unpubl. 2006).

Site Name	Elevation (m)	GPS (UTM's)	Age of exclosure (last year of grazing)	Size of exclosure
Currie	434	10 675164 E 5623113 N	1948	72 m x 32 m
Dewdrop	558	10 667061 E 5625158 N	1972	72 m x 96 m
TMV	882	10 684218 E 5631037 N	1990	~ 100 m x 100 m

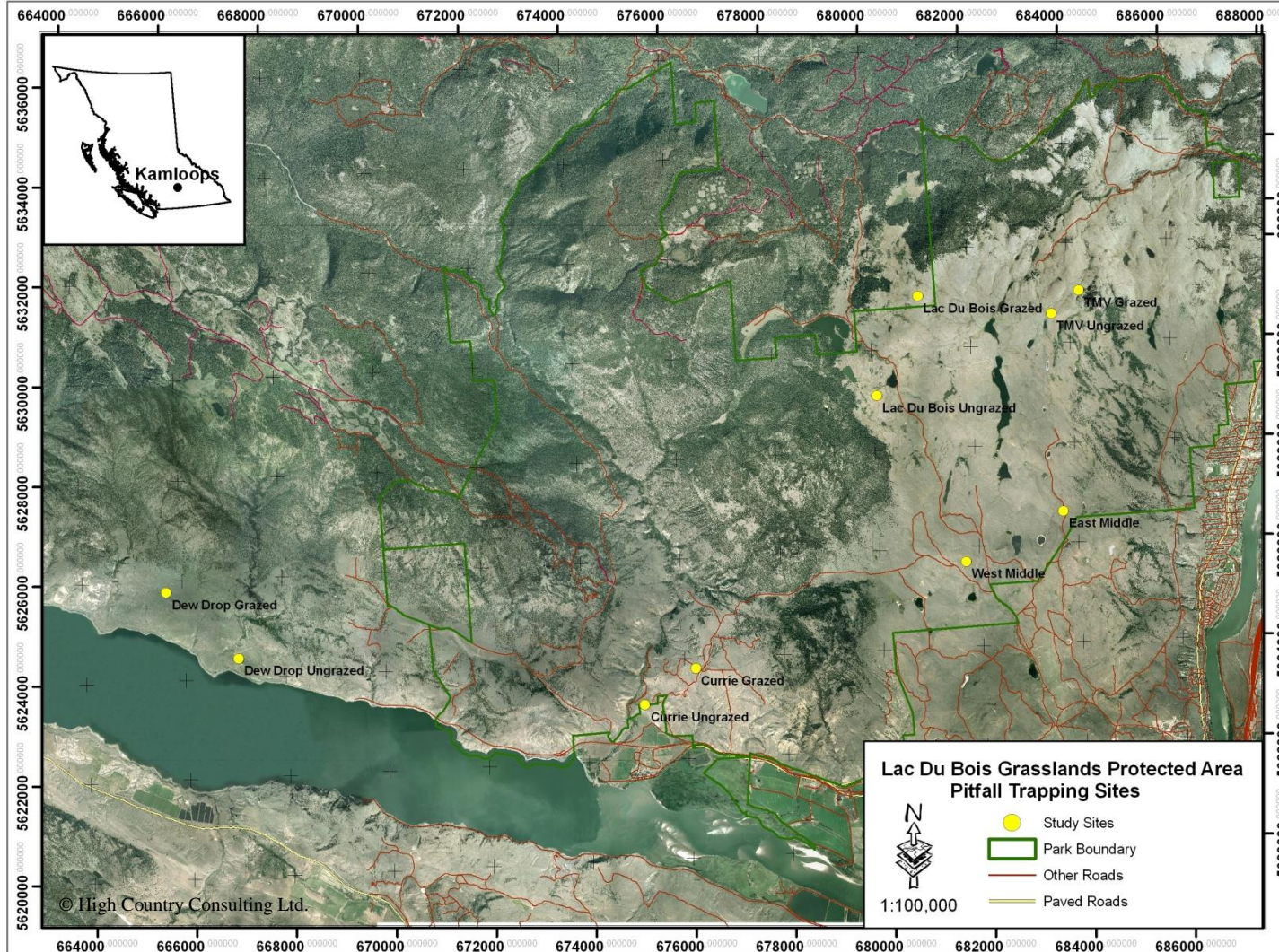


Figure 2.1 Map of sites located in Lac Du Bois Provincial Park near Kamloops, BC. Study site locations are labeled with yellow dots. Sites are either open to cattle grazing (Grazed) or fenced (Ungrazed enclosure).

Vegetation Sampling

Vegetation was sampled in July of 2008. The Daubenmire (1959) method of using a 20 cm \times 50 cm frame was used to visually estimate percent cover of each plant species, bareground, litter, rock, wood, and cryptogammic crust. Daubenmire sampling occurred along three parallel transects with 18 quadrats each for a total of 54 quadrats per site. Each transect was 14.3 m apart, and 71.5 m long (Figure 2.2). Shrub cover was visually estimated with 18 semi-permanent modified Daubenmire sample plots of 3 m \times 3 m, with 6 plots per transect.

Four 1 m² plots along the three parallel vegetation transects were randomly selected and clipped for above-ground litter and live standing biomass samples ($n = 12$ for each site). Biomass and litter were stored in brown paper bags and dried in a Yamato oven (Model No. DKN812) at 65°C for 48 hours and weighed with an analytical balance (Fisher Scientific accuseries 4102).

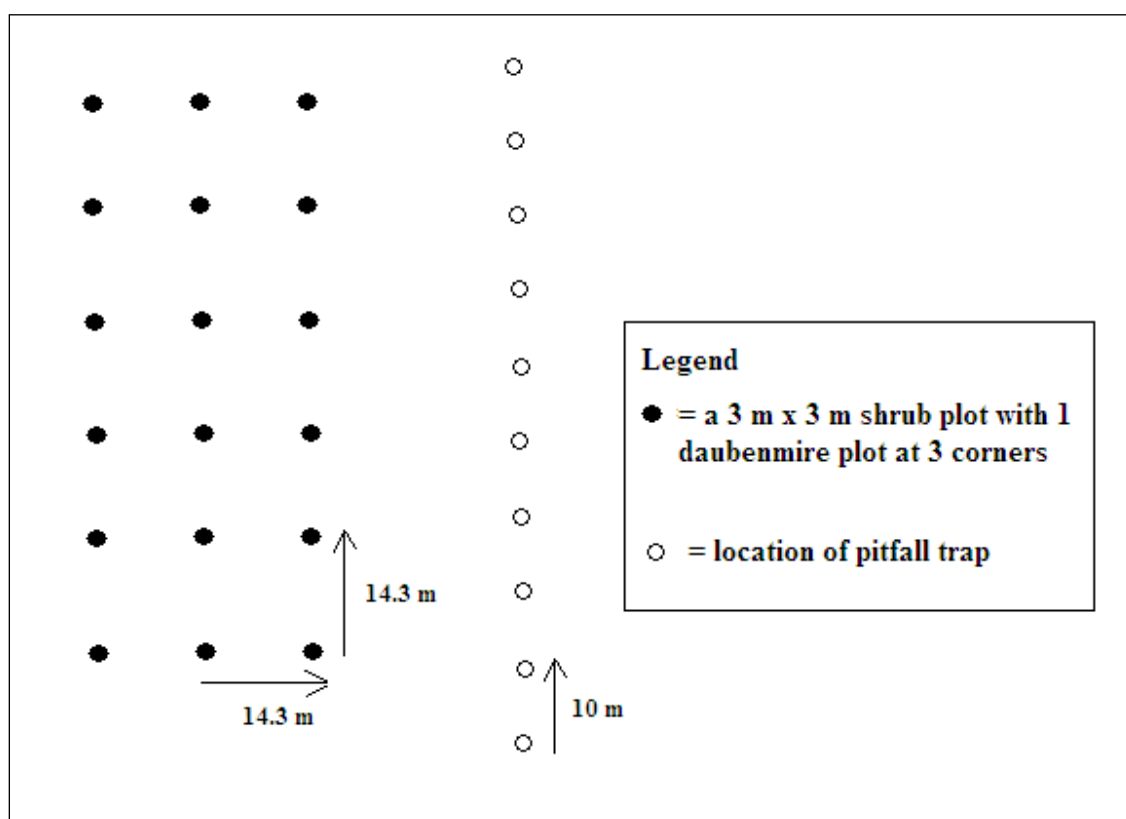


Figure 2.2 Site layout of pitfall traps and vegetation plots.

Insect Sampling Methods

Two methods of insect sampling were used: (1) pitfall traps to catch epigeal insects, namely carabids, and (2) sweep netting to capture insects dwelling on the ground and in vegetation. A preliminary trial of pitfall trapping was completed in July and August of 2007. Refer to Appendix A for sweep net invertebrate abundance, and refer to Appendix B for more detailed information of the 2008 arachnid pitfall captures.

Pitfall trapping

In July 2007 pitfall traps consisting of a dish (50 mm diameter, 30 mm depth) placed inside a cup (95 mm diameter, 97 mm depth) with a funnel were dug into the earth flush with ground level (Brose 2003). To allow for rainwater overflow, two small holes were cut into the bottom of each trap cup. These traps were arranged along a single 100 m transect per site, with one trap every 10 m with at least a 2 m buffer from any fence line and from concurrent small mammal trapping (Figure 2.2). Trap locations were marked with orange flagging tape. Plywood coverboards (30 cm x 30 cm x 4 cm) were placed over each pitfall trap to reduce captures of Orthoptera, Diptera orders and Staphylidae beetles. In 2008, the traps were open for a period of seven days each in May 15 and 16 to May 22 and 23, July 16 and 17 to July 23 and 24, and August 21 and 22 and August 28 to 29. Traps were replaced as needed. To set the trap, the small cup was filled with a liquid solution of 20 ml propylene glycol (MSDS No. 9466107) and 20 ml water (Grandchamp et al. 2005). Samples were collected in Whirl-Paks. Invertebrates were sorted, counted, then stored in 20 ml disposable scintillation vials filled with denatured ethanol. Carabid beetle samples were sorted to species according to Lindroth's (1959) "Carabids of Canada and Alaska". Sample specimens were labeled and pinned.

Sweep netting

A canvas wire-frame 30 cm diameter sweep net was used to capture insects along a 100 m transect, one meter away from, but parallel to the transect of pitfall traps. Two sampling periods were done in July 16 and 17 and August 21 and 22 during mid day with 200 swings of the net over the transect distance (Siemann et al. 1998). Insects were transferred to ziplock bags, stored at cold temperatures, then sorted to order and counted. Representative samples of Hemiptera were pinned and labelled, verified and identified by Dr. Geoff Scudder, professor emeritus at the University of British Columbia.

Statistics and Analysis

Graphs and statistics were completed using R statistical software (R Development Core Team 2005) and Systat 8.0. Due to changes in pitfall sampling methodology I was unable to compare data between the two years. Although in some studies (Kromp 1990; Vanbergen et al. 2005), the numbers from pitfall traps were grouped per site to avoid the potential for pseudoreplication (Hurlbert 1984), many other studies treat pitfall traps as independent (Baars 1979; Desender and Bosmans 1998; Baker and Barumata 2006). In my study, the traps were placed far enough apart (10 m) to avoid differential trap catch (Baker and Barmuta 2006), making it possible to treat each trap as independent.

I used the visual estimates of percent cover to determine the dominant plant species. I used plant species richness in each Daubenmire quadrat to find an average species richness by elevation. A One-Way ANOVA was performed on plant species richness by elevation. Kolmogorov-Smirnov and Shapiro-Wilk tests were used to check plant biomass, plant litter, and carabid dried weight distributions for normality. Plant litter weights were log-transformed to achieve normality. Plant species richness was log+1 transformed. One-way ANOVAs and post-hoc Tukey tests were performed on plant litter weight, plant biomass weight, and plant species richness to test for differences by elevation.

The body length and width of each individual carabid was measured using digital calipers (Marathon CO 030150), then dried for 48 hours at 65 °C in a Yamato oven (Model No. DKN812), and weighed using an analytical balance (Sartorius CP2P). The distributions of carabid body length, and width, and dried weight were tested for normality. *Amara obesa*'s body lengths and dried weights were log-transformed, and two body width outliers were removed to achieve normality. One-way ANOVAs and post-hoc Tukey tests were performed on carabid dried weight, carabid species richness and carabid diversity to test for differences by elevation, fencing, and month. Carabid abundance follows a poisson distribution, and therefore a General Linear Model was used to test for differences by elevation, grazing, and month of capture. The Shannon-Weaver index was used to calculate carabid diversity (Shannon 1948). To test for main and interacting effects, a 3-Way ANOVA was performed with the response variables being carabid abundance, dried weight (biomass), species richness and Shannon diversity by trap, and the factor variables being elevation, grazing, and month of capture. I used Principal Component

Analysis in Systat 8.0 to study the correlations of beetle composition of all pitfall traps to determine whether carabid species assemblages can be clustered into groups and whether those grouping can be explained by either elevation or grazing.

RESULTS

Upper elevation sites were dominated by rough fescue (*Festuca campestris*) (20.3 %), and Kentucky bluegrass (*Poa pratensis*) (14.5 %). Mid and lower elevation sites were dominated by big sagebrush (*Artemisia tridentata*) (13.18 % and 26.99 %, respectively) and bluebunch wheatgrass (*Pseudoroggenaria spicata*) (11.86 % and 15.07 %, respectively). Lower and mid elevation plant communities produced less standing plant biomass ($F_{2,120} = 68.777$, $P < 0.001$) and litter ($F_{2,120} = 37.537$, $P < 0.001$) than upper elevation sites according to One-way ANOVA's and post hoc Tukey tests (Table 2.2). Average plant species richness increased with elevation ($F_{2,540} = 130.94$, $P < 0.001$) (Table 2.2). Plant biomass ($F_{1,120} = 6.99$, $P = 0.009$) and plant litter ($F_{1,120} = 15.021$, $P < 0.001$) were higher in the exclosures (Table 2.2). Plant species richness, however, was lower in the exclosures ($F_{1,540} = 48.215$, $P < 0.001$). Grazing significantly reduced plant biomass at lower and upper elevation sites (Figure 2.3). Grazing significantly reduced plant litter in the upper elevation sites (Figure 2.3).

Six hundred carabid individuals were captured across the three trapping sessions in 2008. Carabid abundance, biomass, species richness and species diversity were highest in the upper elevation sites (Table 2.2, Table 2.3). Fencing increased carabid diversity at upper elevations (Table 2.3; Figure 2.4). Month of capture significantly affected beetle biomass, species richness, and diversity (Table 2.2, Table 2.3). Elevation and month of capture had a significant interacting effect on all carabid response variables (Table 2.3). Elevation and fencing had a significant interacting effect on carabid abundance, species richness and diversity (Table 2.3). Fencing had a moderate effect ($P < 0.1$) on carabid biomass, with more biomass in upper fenced (exclosure) sites (Figure 2.4). Low elevations had the highest species richness in August and Mid elevations had significantly higher carabid abundance, biomass, and species richness in August (Figure 2.5). Upper elevation sites had more carabid biomass in the month of May (Figure 2.5).

Seven species of carabids were identified (Table 2.4). Carabid species abundance varied by elevation (Figure 2.6). Carabid species were significantly different in body length ($F_{5,585} = 9857$,

$P < 0.001$), body width ($F_{5,585} = 2470.3$, $P < 0.001$) and dried weight ($F_{5,585} = 606.71$, $P < 0.001$) (Table 2.4, Figure 2.7).

The first component of the Principal Component Analysis (PCA) explained 22.6 percent of the total variance, and the second component explained 22.0 percent. The first component of the factor loadings plot best explains the variance in beetle species abundance. *Amara obesa* (AOBES) and *Harpalus bicolor* (HBCIO) were clustered together and drive factor one. *Carabus taedatus* (CTAED) and *Cymindis borealis* (CBOR) were clustered together and drive factor two. Upper sites tended to cluster separately from lower and middle sites (Figure 2.8). The PCA scores plotted for the grazing exclosures show that the second component (y-axis, labeled 'Grazing') might be a good indicator for groupings (Figure 2.9).

Table 2.2 Mean values for plant community and carabid community characteristics by elevation (lower, mid, upper), fencing (grazed or enclosure), and month of capture (May, July, August). Values in parentheses are standard error. Bold indicates significant 1-way ANOVAs at the $p < 0.05$ level, and letters represent the significant difference by treatment according to post-hoc Tukey tests.

	Elevation			Fencing		Month		
	Lower	Mid	Upper	Exclosure	Grazed	May	July	August
Plant								
Biomass (g/m ²)	49.856^a (+/- 5.911)	48.928^a (+/- 8.777)	152.073^b (+/- 7.769)	115.238 (+/- 12.312)	79.980 (+/-6.962)	NA	NA	NA
Litter (g/m ²)	44.940^a (+/- 4.875)	30.998^a (+/- 8.017)	208.860^b (+/- 35.163)	171.218 (+/- 44.167)	80.506 (+/-12.181)	NA	NA	NA
Species Richness (20 cm × 50 cm)	2.977^a (+/- 0.102)	4.639^b (+/- 0.144)	5.389^c (+/- 0.123)	3.543 (+/-0.166)	4.587 (+/-0.093)	NA	NA	NA
Carabid								
Abundance per Trap	1.042^a (+/-0.223)	3.250^b (+/- 0.741)	2.875^b (+/- 0.409)	1.789 (+/-0.395)	2.311 (+/-0.286)	1.400 (+/- 0.310)	2.190 (+/- 0.464)	2.690 (+/-0.375)
Biomass per Trap (mg)	25.499^a (+/-7.09)	128.871^b (+/-34.057)	113.706^b (+/-18.507)	66.660 (+/-22.248)	83.474 (+/-10.585)	118.657^a (+/-26.731)	37.957^b (+/- 8.553)	85.711^{ab} (+/-15.786)
Species Richness by Trap	0.458^a (+/-0.061)	1.075^b (+/-0.158)	1.000^b (+/-0.079)	0.756 (+/-0.094)	0.790 (+/-0.061)	0.613^a (+/-0.070)	0.670^a (+/-0.092)	1.002^b (+/-0.090)
Shannon Diversity by Trap	0.061^a (+/-0.017)	0.244^b (+/-0.053)	0.1476^b (+/-0.026)	0.127 (+/-0.029)	0.1224 (+/-0.019)	0.0452^a (+/-0.018)	0.10596^a (+/-0.025)	0.2049^b (+/-0.032)

Table 2.3 Four 3–way ANOVAs comparing the separate and interacting effects of elevation (Lower, Mid, and Upper), month of capture (May, July, August), and fencing (grazed or in exclosures) on carabid beetle abundance, dried biomass, species richness, and Shannon diversity. Bold numbers indicate significance at the $P < 0.05$ level, * indicate significance at the $P < 0.1$ level. (n = 280).

	Abundance		Dry biomass		Species richness		Shannon diversity	
	F	P	F	P	F	P	F	P
Elevation	10.23	< 0.001	21.72	< 0.001	18.96	< 0.001	9.55	< 0.001
Month	1.97	0.141	8.73	< 0.001	6.78	0.001	7.56	< 0.001
Fencing	0.23	0.635	0.92	0.337	3.67	0.057*	3.72	0.055
Elevation × Month	12.21	< 0.001	9.47	< 0.001	7.30	< 0.001	2.70	0.044
Elevation × Fencing	5.00	0.026	3.49	0.063*	9.82	0.002	11.50	< 0.001
Month × Fencing	0.36	0.697	0.47	0.627	0.70	0.498	0.17	0.841
Elevation × Month × Fencing	0.04	0.962	2.10	0.124	1.30	0.274	1.11	0.332

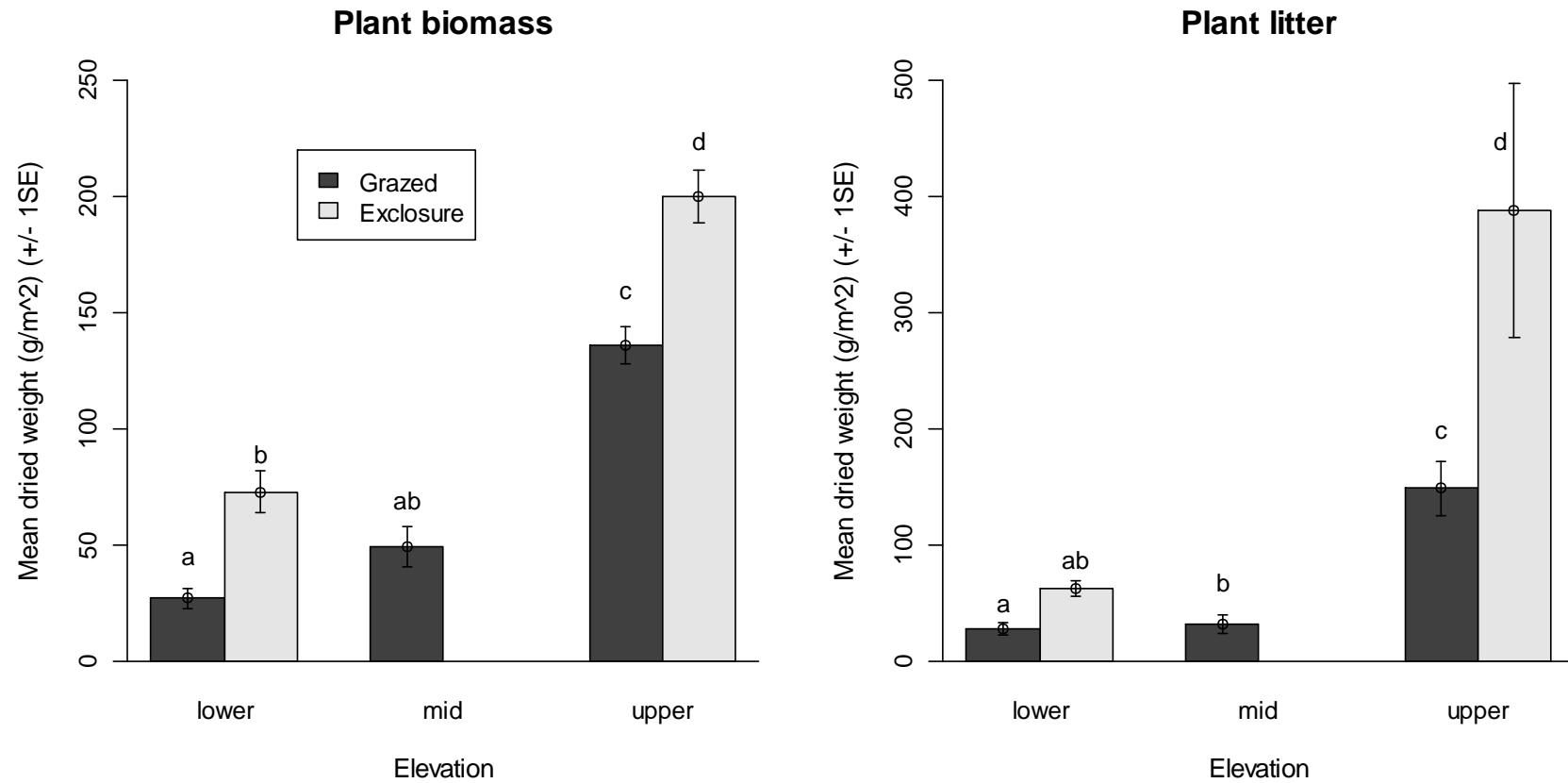


Figure 2.3 Average dried plant biomass (left), and dried plant litter (right) at each elevation in grazed and exclosure (ungrazed) sites. There are no mid elevation ungrazed sites. Bars sharing the same letter are not significantly different using a post-hoc Tukey test.

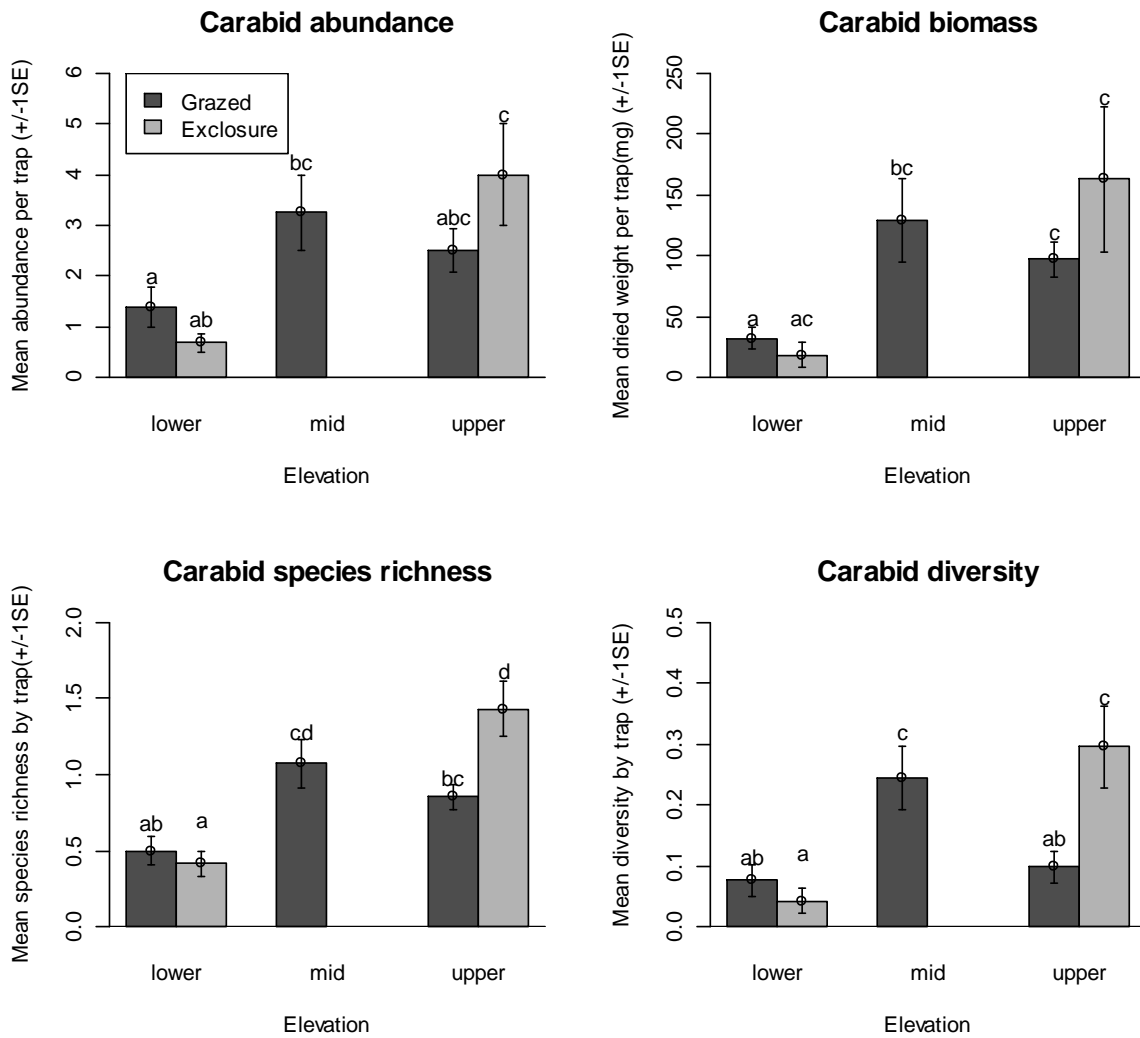


Figure 2.4 Mean carabid abundance (top left), biomass (top right), species richness (bottom left) and diversity (bottom right) at each elevation in grazed and exclosure (ungrazed) sites. There are no mid elevation ungrazed sites. Bars sharing the same letter are not significantly different using a post-hoc Tukey test.

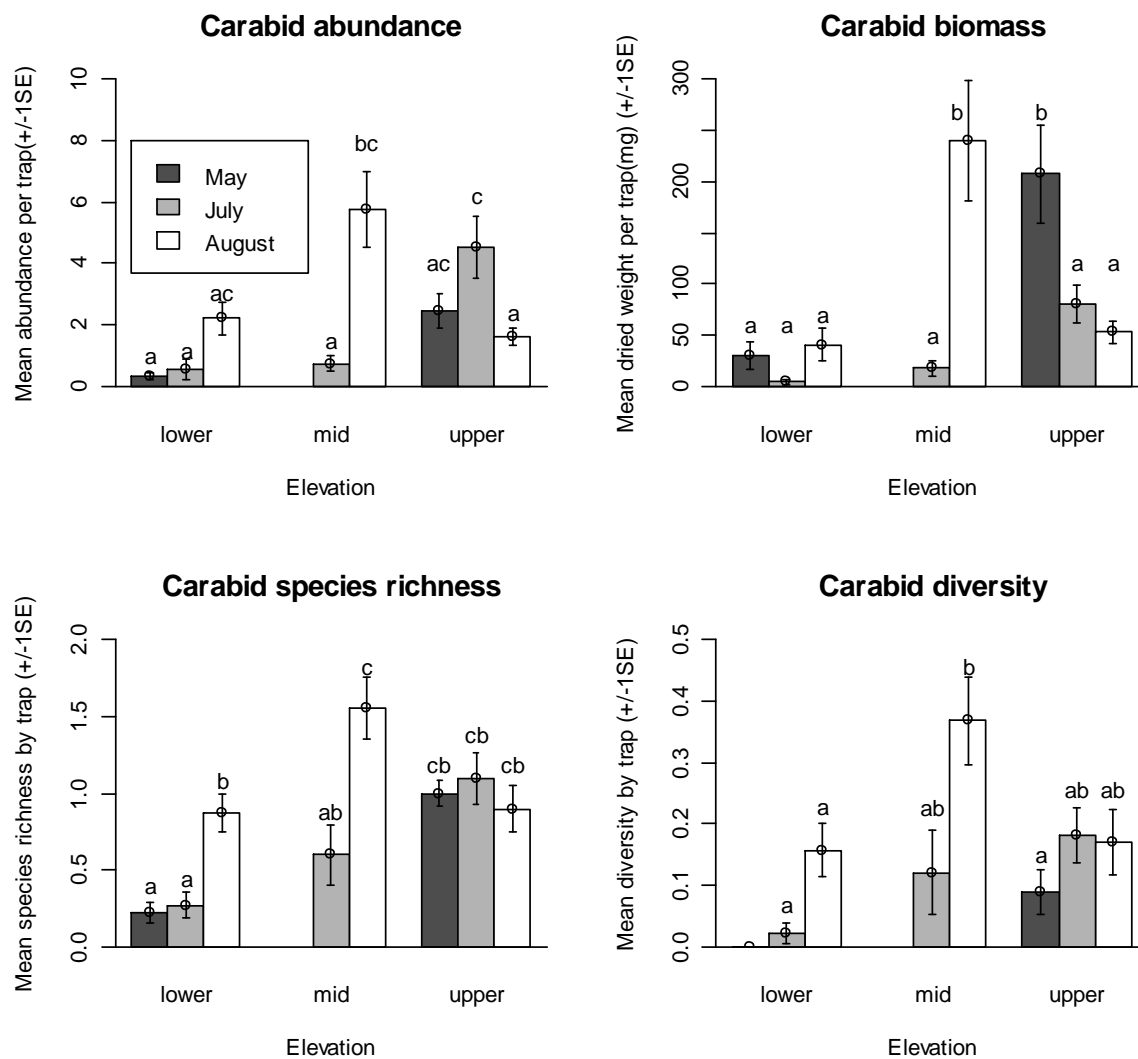


Figure 2.5 Mean carabid abundance (top left), biomass (top right), species richness (bottom left) and diversity (bottom right) at each elevation by month of capture. Mid grassland sites were only trapped in the months of July and August. Bars sharing the same letter are not significantly different using a post-hoc Tukey test.

Table 2.4 Species of carabid beetles captured in study. *= Only found in 2007 preliminary data

Coleoptera : Carabidae
<i>Calosoma wilkesii</i> (LeConte, 1852)
<i>Calosoma moniliatum</i> (LeConte, 1852)
<i>Carabus (Oreocarabus) taedatus taedatus</i> (Fabricius, 1787)
<i>Cymindis (Cymindis) borealis</i> (LeConte, 1863)
<i>Amara (Percosia) obesa</i> (Say, 1823)
<i>Amara (Paracelia) quenseli</i> (Schonherr 1806) *
<i>Harpalus bicolor</i> (Fabricius 1775)

Table 2.5 Average dried weight and body measurements of each carabid species as taken by digital calipers and weighed with an analytical weigh scale. Numbers in parentheses are standard error. Letters represent significance according to a post-hoc Tukey test.

Species	Body length (mm)	Body width (mm)	Dried weight (mg)
<i>Carabus taedatus</i>	22.28 ^a (+/- 0.131)	8.88 ^{ab} (+/- 0.064)	120.52 ^a (+/- 4.59)
<i>Calosoma wilkesii</i>	18.28 ^b (+/- 0.460)	8.86 ^c (+/- 0.005)	70.41 ^{abc}
<i>Calosoma moniliatum</i>	17.60 ^b (+/- 0.116)	7.80 ^{ac} (+/- 0.050)	75.00 ^b (+/- 0.36)
<i>Harpalus bicolor</i>	13.10 ^c (+/-0.365)	5.25 ^d (+/- 0.076)	27.54 ^{cd} (+/- 1.23)
<i>Amara obesa</i>	11.62 ^d (+/- 0.058)	5.12 ^d (+/- 0.024)	13.56 ^d (+/- 0.36)
<i>Cymindis borealis</i>	9.72 ^e (+/- 0.067)	3.58 ^e (+/- 0.020)	6.85 ^{cd} (+/-0.167)

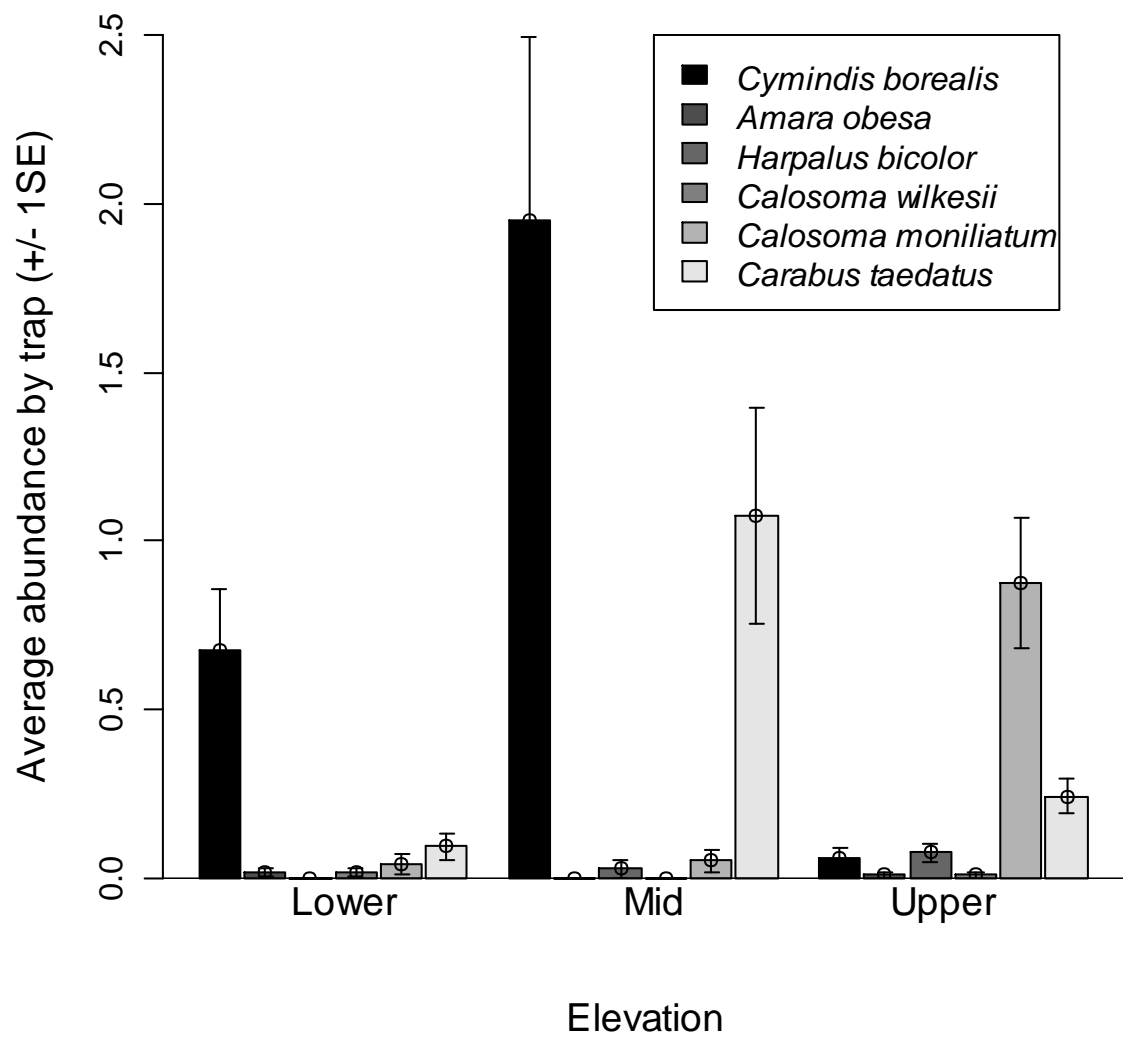


Figure 2.6 Average abundance of each carabid species, grouped by elevation. Species are ordered according to average body size (smallest to largest) from left to right.

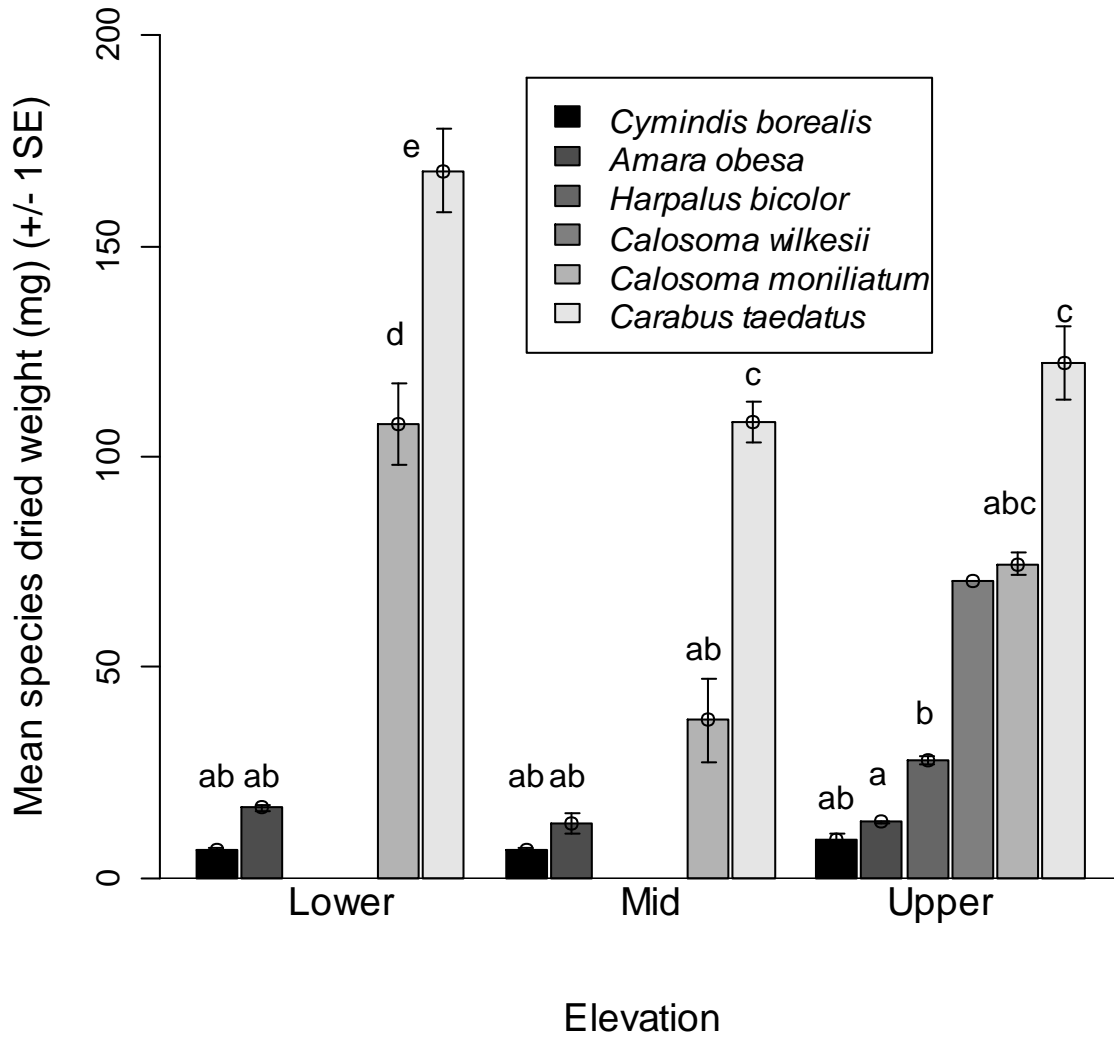


Figure 2.7 Average biomass of each carabid individual by species at each elevation. Species are ordered according to average body size (smallest to largest) from left to right. Bars sharing the same letter are not significantly different using a post-hoc Tukey test.

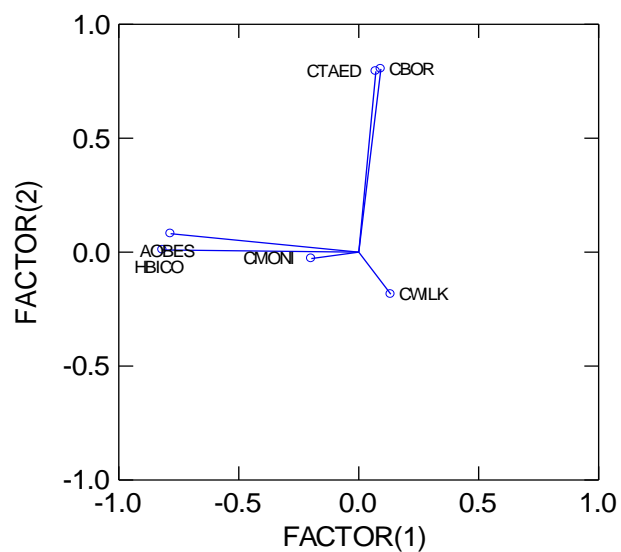


Figure 2.8 PCA analysis factor loadings. Beetle species "CMONI" is *Calosoma moniliatum*, "CWILK" is *Calosoma wilkesii*, "HBICO" is *Harpalus bicolor*, "AOBES" is *Amara obesa*, "CBOR" is *Cymindis borealis*, "CTAED" is *Carabus taedatus*.

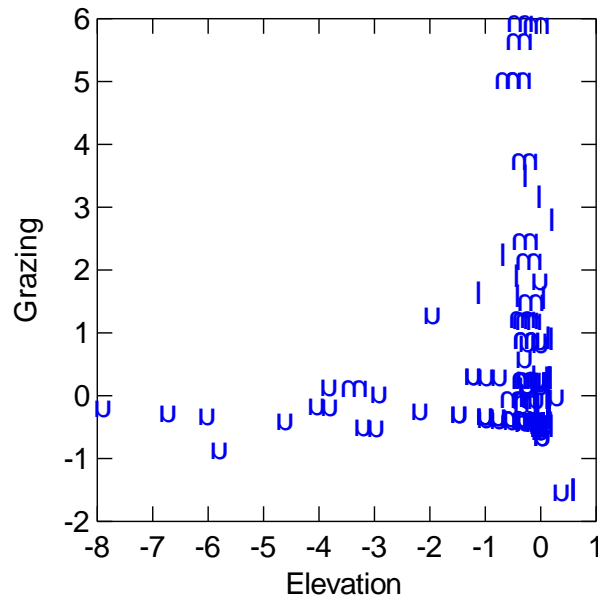


Figure 2.9 Scores from the Principle Components Analysis of carabids. The "u" is Upper elevation, 'm' is the middle elevation, and 'l' is the lower elevation.

DISCUSSION

Carabid abundance, dried weight (biomass), species richness and Shannon's diversity increased with elevation and site productivity, thus providing support for my first hypothesis. The increase in carabid abundance was in agreement with the findings of Siemann et al. (1998) and Patrick et al. (2008), who found that arthropod species richness and abundance was significantly higher in plots with greater plant productivity. The carabid species in my study were either xerophilous, or described as preferring open and sandy soils, with low vegetation (Lindroth 1969). All but one of the carabid species I captured are known to be carnivorous as adults; the exception being *Amara obesa*, a species that is mainly herbivorous as an adult, and eats grasshopper eggs as a larva (Lindroth 1969). Insects can be regulated by plants (Ayal 1994), and will migrate to areas of high food availability (Bohan et al. 2002). Upper elevation sites produced more plant biomass, which possibly provided more food resources for the herbivorous adult *A. obesa*. More than eight times more individuals of *Amara obesa* were captured in the higher elevation grasslands compared to the lower elevation. *Harpalus bicolor* and *Carabus taedatus* followed the same trend with elevation. One species, *Cymindis borealis*, did not follow this trend with elevation, possibly due to a difference in catchability, or a specific preference for the sandy soils and bare ground of lower elevations (Appendix C). Higher carabid abundance in upper elevations could be related to the increase in primary productivity, and corresponding increase in food resource availability; for example the average invertebrate abundance found by sweep net was 34 in lower elevations, and 254.5 in upper elevations (Appendix A). An increase in site productivity, corresponding with higher plant biomass, was correlated with increased carabid beetle biomass and diversity.

The hypothesis that abundance, dried weight, and species richness of carabid beetles would be affected by cattle grazing was not supported. However, carabid diversity was higher in grazed sites compared to ungrazed, which provides partial support for my second hypothesis. Grazing alone seemed to have no affect on carabid abundance. This may be because grazing was moderate, short-term and patchy, providing the opportunity for carabids to migrate and disperse. The trend of lower carabid diversity with grazing is inconsistent with Dennis et al.

(2002) who found a higher diversity of arthropods in light to moderately grazed areas and Crisp et al. (1998) who found high beetle diversity in modified (disturbed) habitats. My results indicate that beetle diversity and abundance are positively correlated with plant biomass, possibly as a result of the increase in height and complexity in plant structure with plant biomass. Since grazing reduces plant biomass, plant height, and plant structure, it is reasonable to conclude that grazing will reduce beetle diversity and abundance, especially if grazing is heavy and consistent.

Carabid abundance was not affected by month of capture, but carabid biomass, species richness, and diversity were significantly altered, thus my third hypothesis was partially supported. It may be that the relative productivity of the rangelands in my study were too low or that seasonal changes in productivity were not significant enough to affect carabid populations. Carabids can be broadly categorized as either breeding in the spring (thus overwintering as an adult), or breeding in the fall (overwintering as juveniles). In general, invertebrate mortality is high due to predation, starvation and disease. Carabid biomass, richness and diversity changes across months are not surprising considering the inevitable fluctuation of spring breeding species and fall breeding species.

Elevation and plant biomass were the most important predictors of carabid abundance, biomass and diversity, and also explained species composition similarities through multivariate analysis. Grazing was an important predictor of carabid communities at high elevation most likely because it reduced the biomass of the plant community. Chase et al. (2000) found that insect biomass increased across a precipitation gradient, with the effect of grazing decreasing with precipitation. The fact that the effect of grazing on carabid community properties in my study increased with elevation, and by proxy precipitation and soil moisture, demonstrates the importance of plant biomass and plant structure. Plant biomass was three times higher at high elevation compared to low elevation in ungrazed sites.

It is perhaps not surprising to find changes in arthropod communities within Lac Du Bois Provincial Park. Roughly et al. (2006) found differences in carabid beetle and spider assemblages within short geographic distances in the forest-aspen ecotone near Winnipeg, Manitoba. Carabids are sensitive to abiotic conditions (Judas et al. 2002). It is important to

note that Lac Du Bois is topographically diverse, with large elevation changes over short distances. Elevation, and the correlated changes in abiotic parameters, affected ground beetle composition in the park. The occurrence of more diverse and abundant populations of carabids in upper elevations might therefore support a more abundant and wider variety of bird and small mammals species.

The conservation of dry grasslands and their carabid populations are important to regional biodiversity and conservation (Desender and Bosmans 1998). British Columbia's grasslands are a proportionally small part of the province, moreover, they are an essential and continually used resource for ranchers, wildlife, and recreation. Biodiversity conservation is an important component of grassland management plans and policy. Carabid abundance, diversity, and biomass do change with elevation – they are affected by grassland site productivity, based on changes along an elevation gradient. Further studies should include the functional characteristics of the insects, or a gradient of grazing intensities.

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CHAPTER 3

Energy Values of Dominant Carabid Beetles and Grass Seeds in a Semi-arid Grassland

INTRODUCTION

All organisms require the capture and assimilation of food for growth, development and reproduction, but not all food resources are of equal quantity and quality. Two food resources for omnivores, granivores and insectivores in the grasslands of British Columbia (BC) are carabid beetles and grass seeds. Carabids and seeds can play an important role in the grassland ecosystem as a food source for ants, small mammals, and birds (Wiens 1977; Mares and Rosenzweig 1978; Agnew et al. 1987). Productivity in the grassland Provincial Park of Lac Du Bois in BC, Canada, change across a gradient of elevation (see Chapter 2).

A measure of food resource quality is the value of energy available expressed in units of calories (Paine 1971; Wiegert and Petersen 1983). Equating the calorific content of samples is an infrequent method in ecological studies. Calorific content can vary between, and among species of plants (Golley et al. 1961). Assimilation efficiency and body size determines species-specific diets of some carabids, and thus carabid species of different sizes may contain different values of calories (Chaabane et al. 1996).

Food for heterotrophs may be limited in amount (e.g., biomass), or quality, or both (Lindeman 1991). Elton's (1927) pyramid, referred to by Lindeman (1991) as the 'Eltonian Pyramid' shows that secondary productivity, the biomass produced by heterotrophs, is limited by the primary productivity of plants, and secondary productivity will always be less than primary productivity due to inefficient transfer of energy. According to the pyramid structure, total biomass or energy of carnivores should be even less than that of secondary producers and primary producers.

Oxygen bomb calorimetry experiments are a way to measure the joules per gram or calories per gram in a sample. This process has been used by Lin and Cao (2008) to measure the

caloric values of forest layers in southwestern China and to compare the allocation of caloric value with different storage strategies. Singh and Yadava (1973) examined the caloric value of tropical grassland plants and insects to test for seasonal variation. Measuring the quality of the food resource of organisms in Lac Du Bois Provincial Park in terms of calories per gram and caloric value may provide insight into the effect of productivity levels on invertebrate populations.

Low elevation grasslands of Lac Du Bois had a mean biomass of 49.86 g/m^2 , whereas upper grasslands had 152.07 g/m^2 (see Chapter 2). According to Elton's theory, there should be a positive relationship between elevation (productivity) and energy. With different levels of productivity, it is important to examine the relationships with biomass and energy (Smith and Walton 1973). Are caloric values of resources the same at different levels of elevation? I addressed the following questions:

1. Do the four dominant carabid species, *Cymindis borealis*, *Amara obesa*, *Calosoma moniliatum*, and *Carabus taedatus*, differ in calories per gram? Does the caloric value of all individuals differ among species?
2. Do seeds of the two dominant grass species of the lower (*Poa sandbergii*, *Pseudorogenaria spicata*) and upper (*Festuca campestris*, *Poa pratensis*) grasslands differ in caloric value per gram? Does the caloric value of all inflorescences differ among species?
3. Does the caloric value of carabids and seeds change along a gradient of elevation?

METHODS

Sample Collection and Preparation

Carabid beetles

Samples of carabid beetles used for oxygen bomb calorimetry were collected in 2008 using pitfall traps (refer to Chapter 2) and sorted to species. Due to the low abundances of some species of carabids, even as low as 5 individuals, I chose to run calorimeter experiments on

four species that had abundances of more than ten individuals; which included *Carabus taedatus*, *Calosoma moniliatum*, *Cymindis borealis*, and *Amara obesa*. From the four species, I randomly chose ten individuals for the calorimetry analyses. To prepare samples of carabid beetle for a calorimeter experiment, a carabid individual (dried and weighed as in Chapter 2), was broken into smaller pieces by grinding it through a stainless steel sieve (aperture 1.00 mm, mesh number 18) and wrapped in a plastic food wrap (I used Saran™ Wrap) to ensure even combustion (as recommended by Jim Davies, pers. comm.. 2007).

Grass seeds

To sample vegetation, I used three transects, with four 1 m by 1 m quadrat frames per transect per site, for a total of 12 quadrats per site. Within this frame, I used a modified Daubenmire (1959) method with a log-scale to measure seed cover. Inflorescences and flowers were then clipped by species, and dried in a Yamato oven (Model No. DKN812) at 65°C for 48 hours and weighed with an analytical balance (Fisher Scientific accuseries 4102). I chose two dominant grass species (bluebunch wheatgrass (*Pseudorogenaria spicata*) and Sandberg's bluegrass (*Poa sandbergii*)) at lower and two (rough fescue (*Festuca campestris*), and Kentucky bluegrass (*Poa pratensis*)) at upper grassland elevations for the calorimetry experiments. Seeds were cut up in a coffee grinder for one minute. The samples were tightly wrapped in Saran™ Wrap to ensure even combustion (as recommended by Jim Davies, pers. comm.. 2007). Average calories per gram of Saran™ Wrap were calculated in separate calorimeter experiments.

Oxygen Bomb Calorimetry

I used two Parr Oxygen Bomb Calorimeters (Model No. 1341EB and Model No. 1341EE). Both calorimeters were calibrated using benzoic acid tablets (Cat No. 3413) (Miller 1997) with a known energy of combustion of -26426 J/g. I used a temperature data logger (Onset HOBO U12 Outdoor/Industrial) to collect temperature of the water every 15 seconds during each experiment. Software HOBOWare Pro (Version 2.3.0) was used to download the data points from the temperature data logger. For detailed methods and calorimetry protocol, refer to Appendix D.

Graphs and statistics were completed using R statistical software (R Development Core Team 2005). The distributions of carabid calories per gram, caloric value of carabids, seed calories per gram, and seed caloric values were tested for normality with Kolmogorov-Smirnov tests. Seed caloric value was log-transformed to achieve normality. A One-Way Analysis of Variance and post-hoc Tukey test was used to examine differences in calories per gram by carabid species, in caloric value of carabids, in calories per gram of seeds by grass species, and in caloric value of grass seeds.

RESULTS

There was a significant difference of calories per gram by carabid species ($F_{3,27} = 3.74$, $P = 0.025$). *Amara obesa* and *Calosoma moniliatum* did not differ significantly in mean calories per gram from the other carabid species (Figure 3.1). However, calories per gram of *Cymindis borealis* were significantly lower than *Carabus taedatus* (Figure 3.1). When average calories per gram for each carabid species was applied to their individual weight (average cal/g \times g), I found that there was a significant difference in the caloric value ($F_{3,508} = 951.01$, $P < 0.001$) among all four carabid species (Figure 3.2).

Grass seed caloric value was log-transformed to meet the assumptions of ANOVA. Grass seeds did not differ in mean calories per gram by species ($F_{3,34} = 0.18$, $P = 0.543$) (Figure 3.3). When average calories per gram for the four grass species was applied to the weight of each tiller of that species (average cal/g \times g), I found that the two dominant upper elevation grasses had much greater caloric value than two dominant lower elevation grasses ($F_{3,157} = 24.21$, $P < 0.001$) (Figure 3.4).

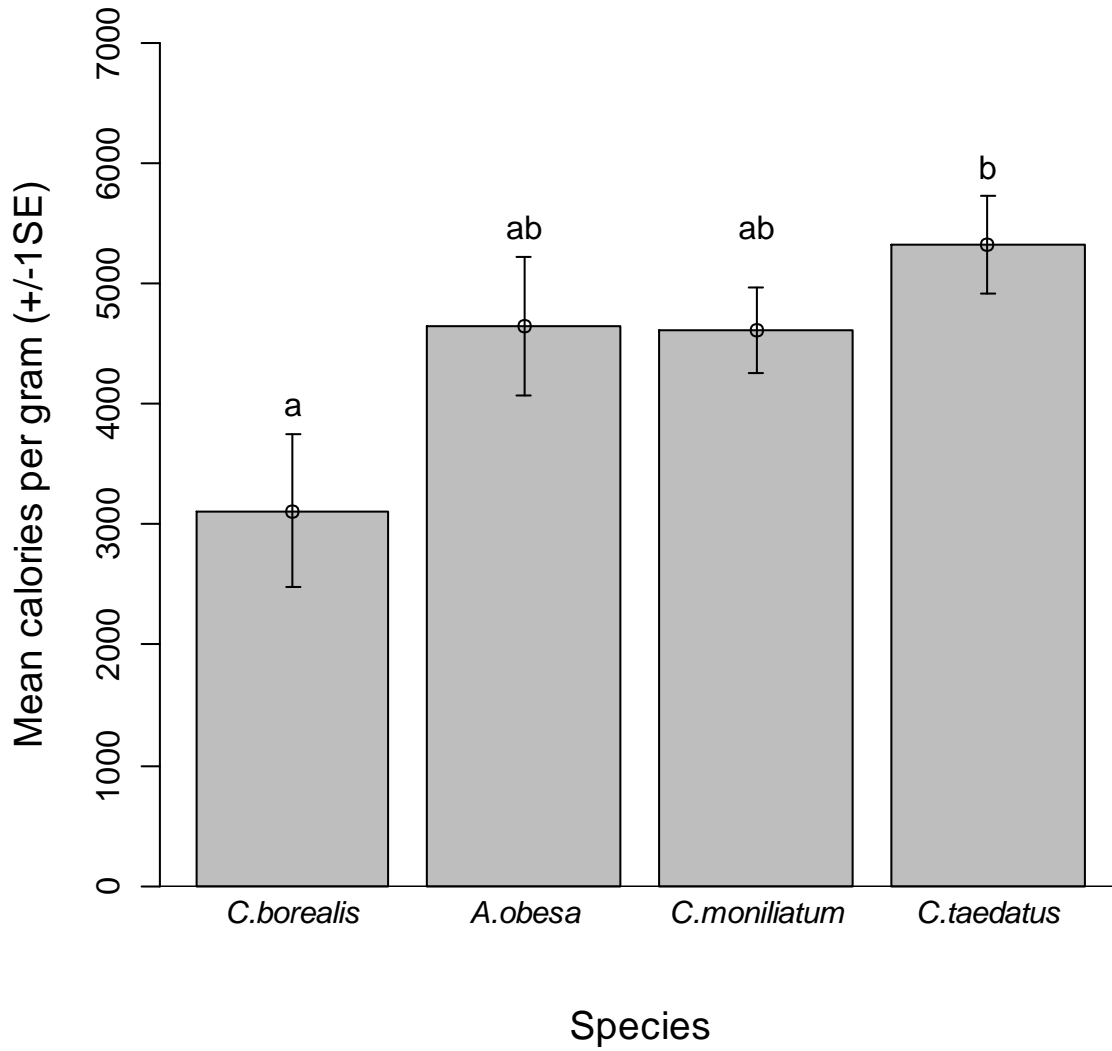


Figure 3.1 Mean caloric value per gram of four carabid species. Bars sharing the same letter are not significantly different using a post-hoc Tukey test.

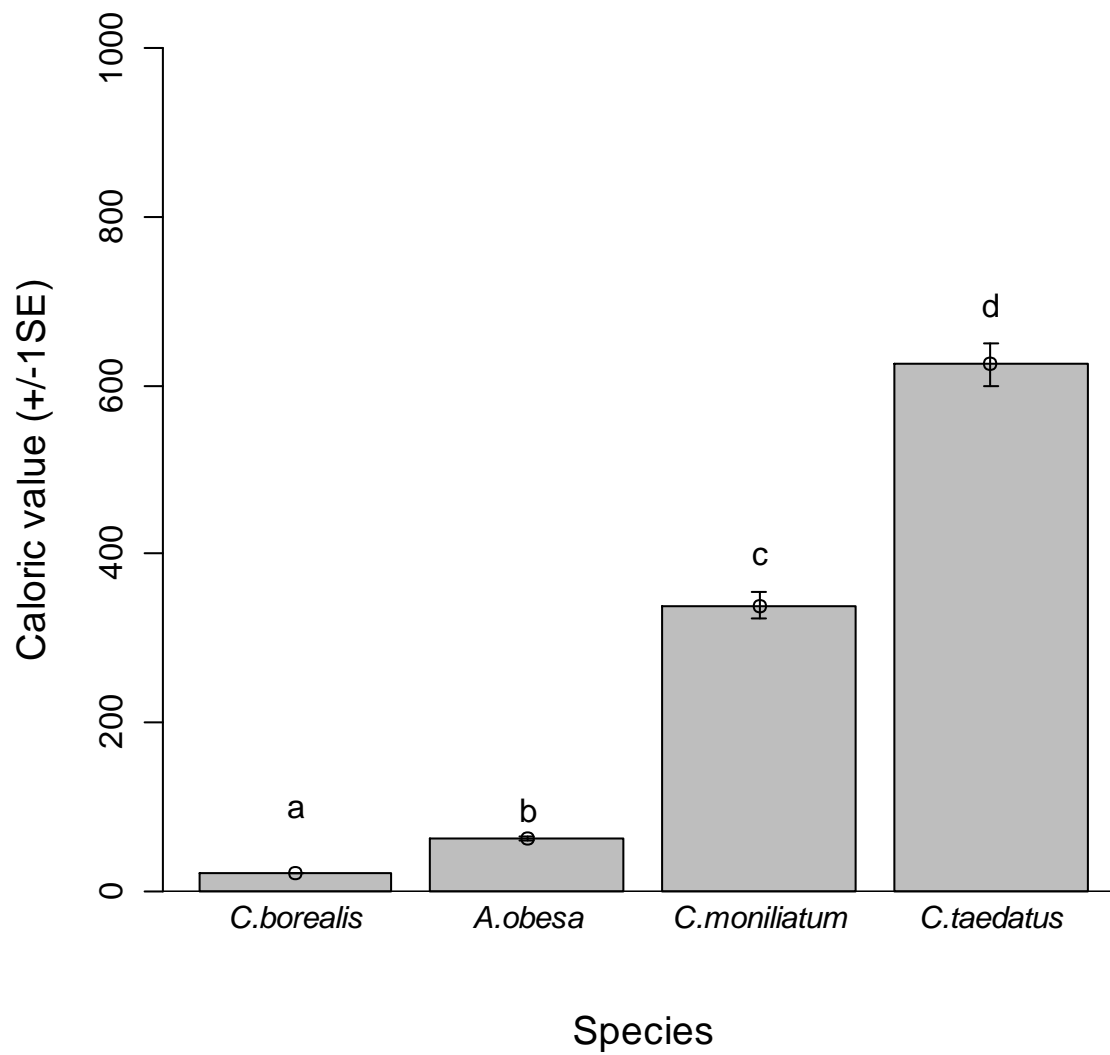


Figure 3.2 Caloric value by species. Bars sharing the same letter are not significantly different using a post-hoc Tukey test.

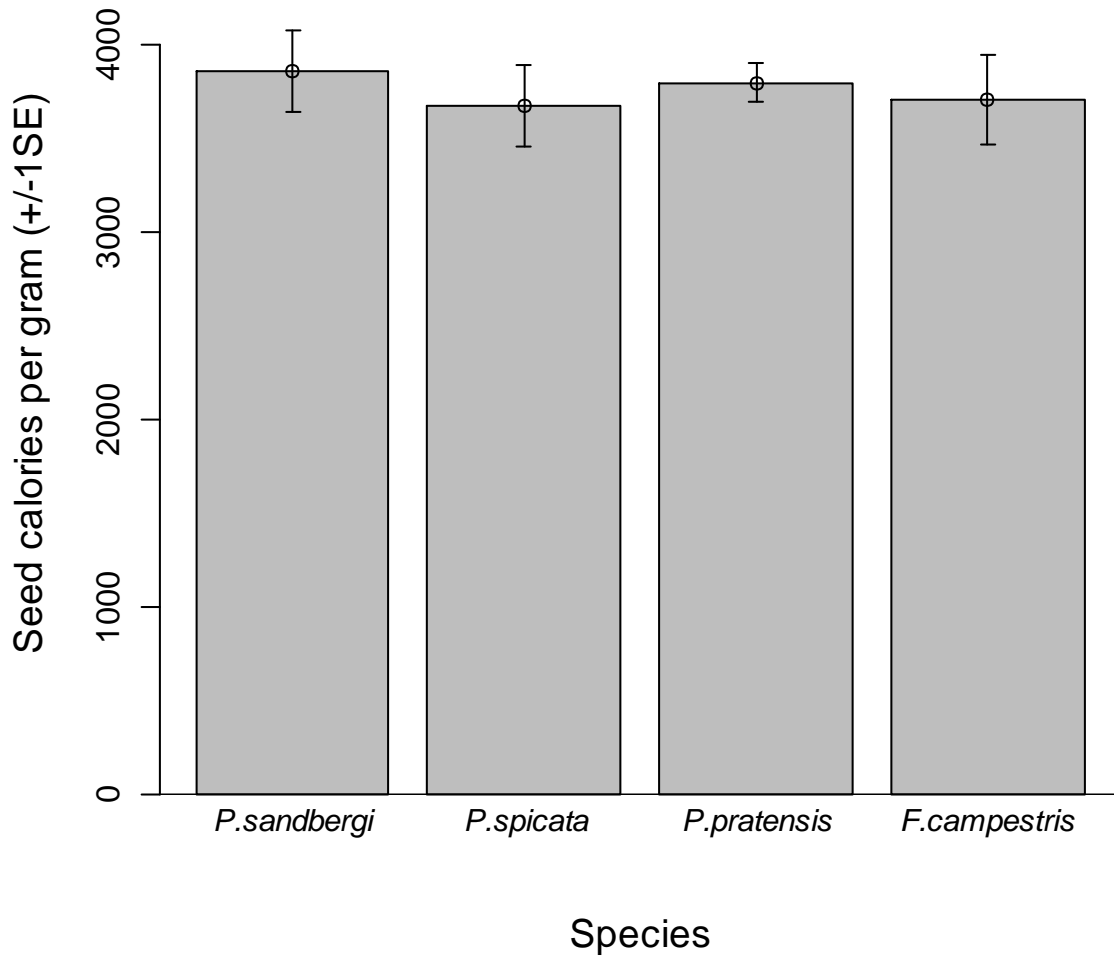


Figure 3.3 Mean calories per gram of the seeds from Sandberg's bluegrass (*Poa sandbergii*), bluebunch wheatgrass (*Pseudorogenaria spicata*), Kentucky bluegrass (*Poa pratensis*), and rough fescue (*Festuca campestris*).

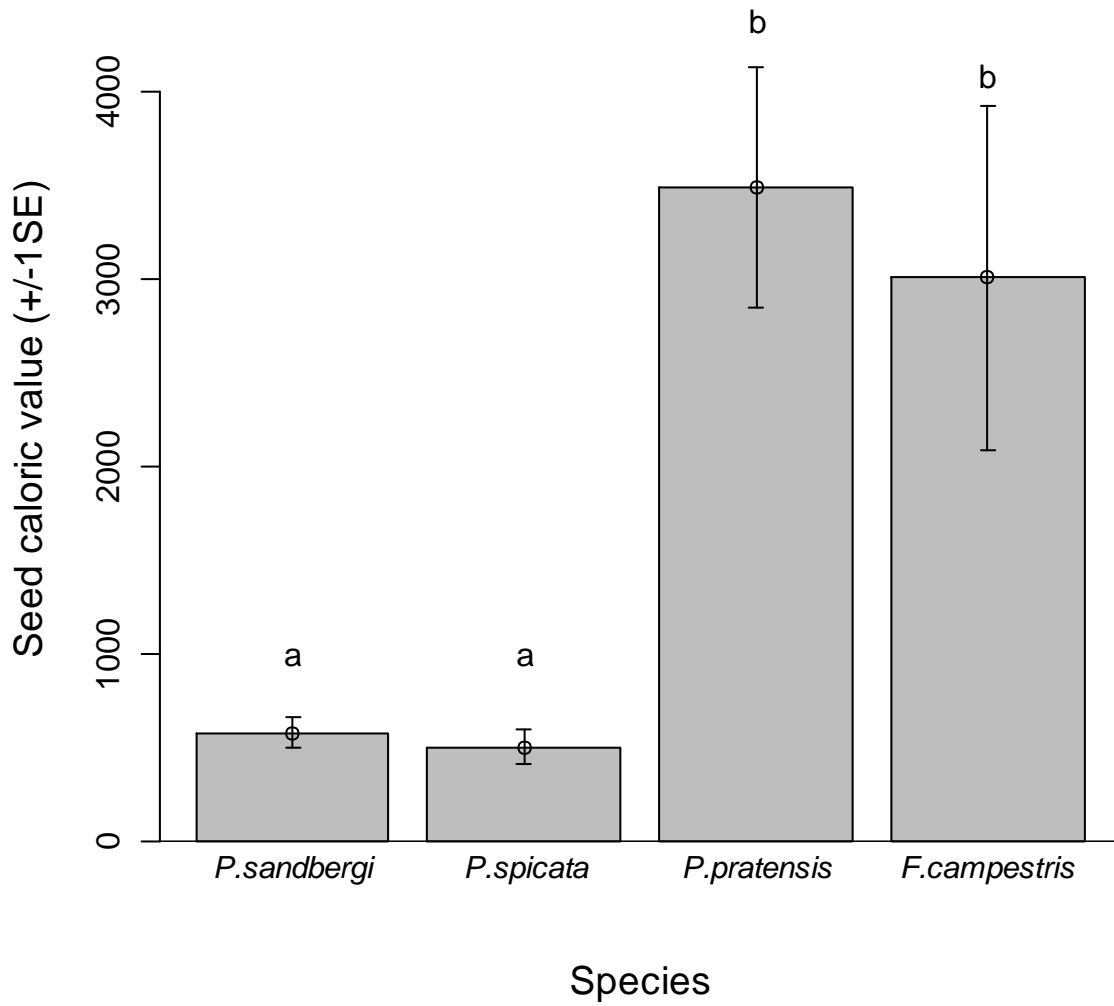


Figure 3.4 Caloric value as found by applying the mean calories per gram to the tiller weights of each grass species of Sandberg's bluegrass (*Poa sandbergii*), bluebunch wheatgrass (*Pseudorogenaria spicata*), Kentucky bluegrass (*Poa pratensis*), and rough fescue (*Festuca campestris*). Bars sharing the same letter are not significantly different using a post-hoc Tukey test.

The energy value of grass seed was high in the upper grasslands, low in the lower grasslands, and the lowest in the middle grasslands (Figure 3.5). *Festuca campestris* did not occur in the lower or mid grassland sites, *Poa pratensis* did not occur in the lower grassland sites, and *Poa sandbergii* did not occur in the upper grassland sites. The trend of total carabid caloric energy is from lower > mid > upper elevations (Figure 3.6). This result underestimates the caloric energy of beetles at mid elevations, because mid elevations were only sampled twice for carabids, while upper and mid elevations were sampled three times during the year. *Carabus taedatus* and *Calosoma moniliatum* constitute a large portion of the total caloric energy.

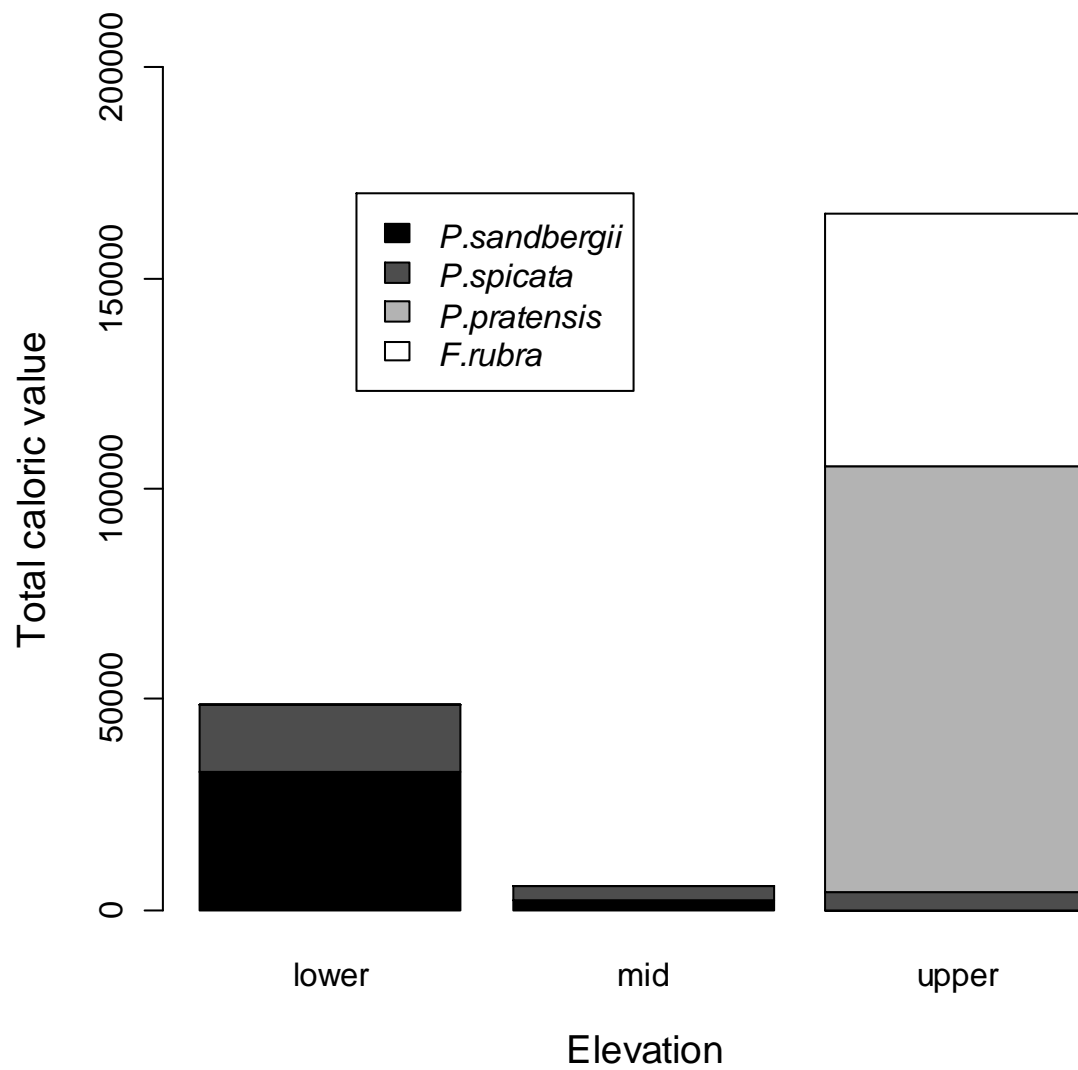


Figure 3.5 Sum of the caloric value (calories \times calories per gram) of the dominant species of grassland seeds at each elevation.

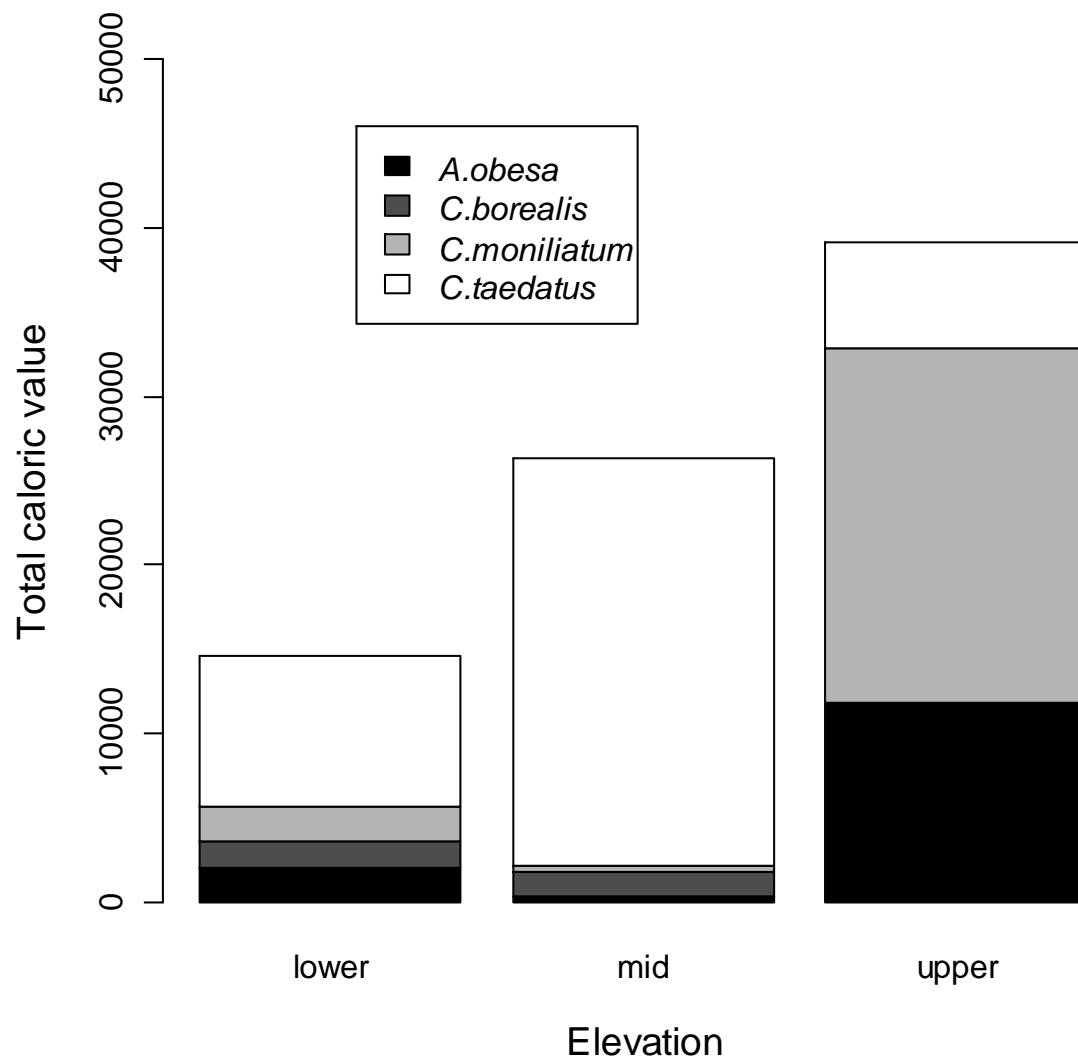


Figure 3.6 Sum of the caloric value (calories \times calories per gram) of dominant carabid species at each elevation.

DISCUSSION

I found that the average calories per gram of *Carabus taedatus* was higher than that of *Cymindis borealis*, thus providing support for my first hypothesis. The variation in calories per gram among carabid beetle species could be explained by seasonal variation of energy density, as found in carabids by Chen et al. (2004). I expected to find significant differences in the calories per gram by species because Carabidae can differ physiologically; *Carabus taedatus* can secrete a defensive compound called methacrylic acid (Benn et al. 1973) whereas other species may rely on non-chemical defenses. Carabidae can also have species-specific diets due to body size and corresponding assimilation efficiency (Chaabane et al. 1996).

By multiplying individual body mass (dried weight in grams) of all carabid individuals of those species by the mean species calories per gram to get caloric value, I found that the carabid species with a larger body size also contain higher caloric value, and provide the most caloric value at each elevation despite lower average abundances. Optimal Foraging Theory (Stephens and Krebs 1986) suggests that larger sized carabid species with more calories (*Carabus taedatus*) should be a more worthwhile food resource than smaller sized species (*Cymindis borealis*). If selective insectivory occurs, it is reasonable to presume that the larger, energy-rich *C. taedatus* would prefer dense vegetation as an enemy-free space (Brose 2003), and require strong pygidial defensive secretions as protection from predators. The upper grasslands, where the majority of *C. taedatus* were found, provided more plant biomass and cover than the lower grasslands (see Chapter 2).

My hypothesis of grass seeds being significantly different in calories per gram was not supported. I expected to find that grass species would differ in caloric value per gram due to the fact that grassland seeds can differ widely in nutritive value (i.e., carbohydrates and proteins) by species (Kelrick and MacMahon 1985; Kelrick et al. 1986). Energy on a per gram basis is not as important for grass seed selection by granivores as other seed qualities such as size, availability, and defensive traits. Although productivity levels in terms of plant biomass do differ by elevation (see Chapter 2), seed resources on a per gram basis of dominant grass species are not higher at the upper, more productive grassland elevation.

The average caloric value of each seed species was lower than the caloric value of seeds as reported by Golley (1961), who found that plant seeds ground and pooled from random plots contained 5065 calories. It is important to consider the quality of grass seed as a food resource. Wenninger and Inouye (2008) found that food resource components in a sagebrush-steppe ecosystem, such as plant quality and abundance, were a major driver in structuring insect communities, even more so than moisture treatments (spring irrigation, summer/fall irrigation, ambient precipitation). Dominant grass species in the upper grasslands (*Pseudorogenaria spicata* and *Poa pratensis*) produce more grams of seed, therefore even though on a per gram basis, grass seeds in lower and upper elevations are equal, upper elevations provide more abundance of seed 'food' energy. Upper elevations may therefore be able to provide for a more diverse and abundant granivore population. *Festuca campestris* is known to mast irregularly, such that in one year *F. campestris* may produce a large batch of seeds, and years may pass before another large mast is produced (Anderson 2006). In 2008, a large mast of fescue seed was produced (Rick Tucker, pers. comm.), the irregular production of seed may be a factor in the population fluctuations of granivorous insects. The total caloric value of the seed of dominant grass species may be lower in upper grasslands in future years due to this irregularity.

Future studies of oxygen bomb calorimetry should include non-dominant grass species, forbs, or sagebrush, and should capture carabid beetles without the use of chemicals for preservation. It would also be useful to take a more accurate measurement of seed production on the landscape, and examine the harvesting of seed at different trophic levels, for example by ants (Appendix C), rodents, and birds.

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CHAPTER 4

Synthesis and Implications for Management

INTRODUCTION

The southern interior grasslands of British Columbia (BC), Canada are home to many rare and endangered grassland wildlife species, important for the preservation of biodiversity and for monitoring environmental change (Henwood 1998). Grasslands provide resources for many blue and red-listed species (Gayton 2003). Semi-arid grasslands in BC are water limited (Tisdale 1947; van Ryswyk et al. 1966). In the grasslands of Lac Du Bois Provincial Park, elevation changes with a concurrent precipitation gradient is a major factor that leads to the development of different plant communities along a gradient of productivity.

I monitored changes in rangeland insect communities over time at different levels of productivity, and with the impact of cattle grazing. Four hypotheses were made about carabid responses to grassland elevation, grazing, and month. My first hypothesis that carabid abundance, biomass, species richness and diversity increases with productivity was supported. My second hypothesis that abundance, dried weight, species richness and diversity of carabid beetles would be affected by cattle grazing was not supported except in the case of carabid diversity. Carabid abundance was not affected by month of capture, but carabid biomass, species richness, and diversity were significantly different, thus my third hypothesis was not supported. I found interacting effects of grazing and elevation, and of elevation and month of capture.

I calculated the calories per gram and caloric value (calories per gram \times grams in sample) of four carabid species and four dominant grass species. My first and second hypotheses were supported: two carabid species were significantly different in their calories per gram, and all species were significantly different in their caloric value. Large sized carabid species represented a significantly larger proportion of carabid biomass, and caloric value even at low abundances. Thus it is important to consider the conservation of large body sized carabid species in semi-arid grassland regions due to their potential contribution to the food web. My

third hypothesis was not supported - all four grass species did not differ significantly in calories per gram of seed. My fourth hypothesis was supported: upper elevation dominant grasses produced significantly more seed caloric energy than lower elevation dominant grasses. A more abundant availability of caloric resources in the upper grasslands may provide more resources to support higher trophic levels, such as hemipterans, ants, small mammals, and birds (Fretwell 1987).

FUTURE DIRECTIONS

My research tested aspects of beetle community assemblages in grasslands. My study has also provided important baseline information for future research in grassland communities. There are limitations to the conclusions that can be drawn from a small number of sampling sessions of pitfall trapping. There can be pitfall trap bias due to different catchability of species, initial disturbance of digging-in traps, or from the introduction of coverboards (Greenslade 1964). There may have been bias in the oxygen bomb calorimetry experiments due to the previous storage of insects in ethanol. It may be more appropriate to aim for complete ash-free dried weight of carabids, by titrating the washings of the crucible post-detonation. Plant standing biomass, litter, and seed collection only occurred once throughout the year. The timing of this sampling may have caused me to have an inaccurately low number of spring annuals. The function and structural complexity of shrubs such as big sagebrush (*Artemisia tridentata*) was overlooked.

The findings of this study may be useful to make predictions in future studies. Some taxa of invertebrates follow the same trend of carabid beetles in terms of abundances by elevation (Appendix A; Appendix B), whereas spiders (Araneae) exploit the same resources as carabids but do not follow this trend. Due to the higher abundance and diversity of carabids, and larger resource of caloric value in the upper elevation grasslands, one would expect to find a more abundant vertebrate population inhabiting the area. Grassland invertebrate research is a necessary component to the understanding of community ecology and management of semi-arid grasslands.

IMPLICATIONS FOR MANAGEMENT

Grasslands tend to experience a high degree of destructive alteration from tourism, urban development, and industrialization. Global climate change may increase risk of species extinction, especially those of limited mobility and of limited range (Vié et al. 2009). It is therefore important to collect baseline data on species of limited mobility that live in semi-arid grassland areas, such as the carabid beetle populations in the southern interior grasslands of British Columbia. There is potential for the use of carabid beetles as a study organism and bioindicator in the conservation and management of temperate grasslands, especially in multi-use areas with a range of management concerns: saline pond degradation, all-terrain vehicle use, wildlife, cattle, tree encroachment, fire suppression, urbanization.

The majority of grasslands in British Columbia are managed for cattle grazing. The elevation gradient and associated grassland types found within Lac du Bois Provincial Park represent a wide range of typical grasslands found throughout the province. My results suggest that high elevation, high productive grasslands support a higher abundance and diversity of carabids than low elevation grasslands, and that grazing at high elevations may lead to a reduction in diversity of carabids. Grazing at lower elevation grasslands did not seem to have any effect on abundance and diversity of carabids. If the goal of management is to increase biodiversity, it is important to consider strategies to reduce the impact of grazing on carabid populations in high elevation grasslands. Since there is a positive correlation between vegetative biomass and structure and carabid populations it would be constructive to investigate a possible threshold of vegetative grazed stubble height so that grazing can occur but a safe habitat is still provided for carabids.

Within the Lac Du Bois Grassland Park of British Columbia, plant and invertebrate species composition and biomass vary along a gradient of elevation, and my findings suggest that it is useful to relate these differences in terms of energy values. Grass seeds and carabid beetles are important components of the grassland food web. Seeds, as an energy rich part of plants, are a small part of the diet of large grassland mammals. Furthermore, seeds are a main part of the diet of many birds, small mammals, and insect groups (Janzen 1971, USA Army Center for Health Promotion and Preventative Medicine 2004). Carabids have more caloric value in

upper grasslands, and this trend could be true for other important taxon such as Hemiptera (Appendix A) and ants (Hymenoptera: Formicidae) (Appendix B), as both appear to occur in higher numbers at upper elevations. *Poa pratensis* contributes a significant amount of caloric value to the upper grasslands therefore maintaining production of this species may an important source of energy for local and migratory omnivore populations.

There is an irreversible global species richness decline caused by human activities (Chapin III et al. 1998). In British Columbia, Canada, grasslands are important areas of high species richness and diversity (Gayton 2003). Grassland management as it pertains to biodiversity needs to consider the importance of invertebrates, not just vegetation and mammals. Plants and carabids produce relevant amounts of caloric energy, and thus play an important role as a food resource in maintaining populations of higher trophic levels. Agnew et al. (1987) found that Carabidae can be a large component of small mammal diets in prairie grasslands. Predacious invertebrates, which include carabids, can provide between 5-15% of the diet of grassland bird communities (Wiens 1977). Red and blue listed species in BC such as the flammulated owl (*Otus flammeolus*), long-billed curlew (*Numenius americanus*) and sharp-tailed grouse (*Tympanuchus phasianellus*) rely on the semi-arid grasslands, and directly or indirectly use these caloric resources. Invertebrate diversity monitoring and the valuation of food energy are useful components of sustainable grassland management.

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APPENDIX A

Sweep-net sampling. Summary of the total number of individuals captured in each insect order. * = only sampled in July and August.

ORDER	Currie		Dewdrop		East	West	LDB	LDB	TMV	TMV
	Fenced	Grazed	Fenced	Grazed	mid * Grazed	mid * Grazed	Grazed	Hill Grazed	Fenced	Grazed
<i>Orthoptera</i>	0	1	0	6	6	0	2	5	1	0
<i>Odonata</i>	0	0	0	1	0	0	0	1	0	4
<i>Coleoptera</i>	11	6	19	1	5	3	25	8	5	6
<i>Dermaptera</i>	0	0	0	0	0	0	0	0	0	3
<i>Diptera</i>	33	1	4	16	33	7	76	37	140	76
<i>Hemiptera</i>	3	3	16	40	67	5	14	137	495	381
<i>Hymenoptera</i>	25	4	27	8	52	8	37	3	8	25
<i>Lepidoptera</i>	1	0	6	5	0	2	0	1	1	0
<i>Neuroptera</i>	0	0	1	0	0	0	0	0	1	0

APPENDIX B

Pitfall trapping. Summary of the total number of individuals captured of ants (*Hymenoptera: Formicidae*), darkling beetles (*Coleoptera: Tenebrionidae*) and spiders (*Arachnida: Araneae*). * = only sampled in July and August.

Order	Family	Currie	Currie	Dewdrop	Dewdrop	East	West	LDB	LDB	TMV	TMV
		Fenced	Grazed	Fenced	Grazed	mid Grazed	mid Grazed	Grazed	Hill Grazed	Fenced	Grazed
<i>Hymenoptera</i>	<i>Formicidae</i>	142	60	163	77	286	687	450	127	99	498
<i>Coleoptera</i>	<i>Tenebrionidae</i>	34	40	21	27	21	18	142	13	2	0
<i>Arachnida</i>	<i>Araneae</i>	113	66	57	68	53	53	36	70	122	59

APPENDIX C

Ground cover of each site sampled during Daubenmire vegetation sampling. Cryptogrammic crust was considered both mosses and lichens, coarse woody debris (CWD) was considered any sticks or twigs with a diameter larger than 1 cm.

	Currie Fenced	Currie Grazed	Dewdrop Fenced	Dewdrop Grazed	East mid Grazed	West mid Grazed	LDB Grazed	LDB Hill Grazed	TMV Fenced	TMV Grazed
Bare Ground	19.05	30.52	15	15.41	14.259	33.72	1.76	0.537	0.67	3.81
Rock	0.35	2.24	8.75	2.41	14.65	5.54	0.84	0.11	0.189	2.07
Cryptogrammic Crust	32.11	28.48	31.38	28.81	32.962	17.67	18.22	6.48	4.53	17.67
CWD	5.46	6.5	5	8.277	0.33	7.91	0	0	0	0

APPENDIX D

Protocol and Methods of Oxygen Bomb Calorimetry Experiments on Carabid Beetles and Grass Seeds

INTRODUCTION

Calorimetry is the measurement of the heat released during combustion, and can be used to calculate the primary energy available in an organism. Oxygen bomb calorimetry experiments involve the combustion of a sample in a constant volume system. When an electric current ignites the sample, it combusts almost instantly and thus releases heat. This heat changes the temperature of a surrounding water bath, and is recorded and used to calculate the amount of energy released.

Oxygen bomb calorimetry is a way to quantitatively measure the energy value differences of organic samples. The caloric value quantifies the primary energy available to important grassland organisms, such as deer mice, and birds. Grass seeds and carabid beetles are important components of energy flow in grassland ecosystems. Oxygen bomb calorimetry experiments are used to compare caloric values of four species of carabid beetles, and the seed of four grass species.

There are some known limitations to oxygen bomb calorimetry. Carabid samples were previously stored in ethanol and as such, may not a completely accurate representation of caloric content. It is also important to note that the energy value (J/g and cal/g) reported is not the value of what an organism would receive from digesting a carabid beetle or seed, due to the indigestibility of some compounds, such as chitin, which is indigestible except by some fungi and bacteria (Schrempf 2001).

Oxygen Bomb Calorimetry

I was able to use two Parr Oxygen Bomb Calorimeters (Model No. 1341EB and Model No. 1341EE) to conduct calorimetry experiments on organic samples. I calibrated both calorimeters using benzoic acid tablets (Cat No. 3413) with a known energy of combustion of -26426 J/g. I set up a temperature data logger (Onset HOBO U12 Outdoor/Industrial) to

collect temperature of the water every 15 seconds during each experiment. Software HOBOWare Pro (Version 2.3.0) was used to download the data points from the temperature data logger. There were four components of each oxygen bomb calorimetry experiment: sample preparation, pre-detonation, detonation, and post detonation.

Sample preparation

To prepare samples of carabid beetle for a calorimeter experiment, a carabid individual (dried and weighed as in Chapter 2), was broken into smaller pieces by grinding it through a stainless steel sieve (aperture 1.00 mm, mesh number 18). Seeds were cut up using a coffee grinder for one minute. The samples were tightly wrapped in Saran Wrap to ensure even combustion (as recommended by Jim Davies, pers. comm.. 2007). Average calories per gram of Saran Wrap were calculated in separate calorimeter experiments.

Pre-detonation

The prepared sample was placed inside the crucible in the bomb reaction chamber (Figure D.1). Ten centimeters of iron fuse wire (No. 45C10) (with a known energy of combustion of - 6694 J/g) was weighed, connected to the electrodes, and bent in a “V” shape to make contact with the sample inside the crucible. The oxygen bomb was then closed, filled with 30 atmospheres of oxygen (99.995 % purity) and placed inside a chromium plated bucket, inside an insulating jacket. The chromium plated bucket was filled with 2 L of water at 25 °C +/- 0.5 °C. The insulating jacket was closed with a lid, and a motorized stirrer turned on to keep the water moving during the experiment.

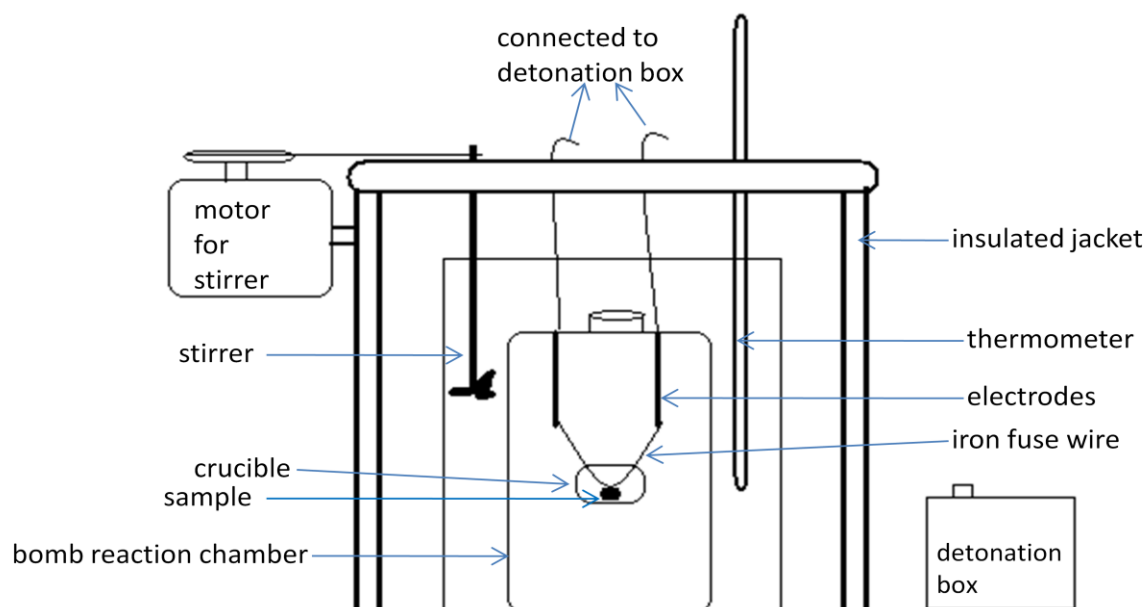


Figure D.1. Diagram of an oxygen bomb calorimeter.

Detonation

One minute prior to detonation, the bomb ignition unit was connected to the calorimeter, and connected to a power source. The detonation button was pressed, to send an electric current through the iron fuse wire to ignite the sample inside the oxygen bomb.

Post-detonation

Post detonation, the temperature data logger recorded for twenty minutes. The post-detonation temperature was graphed to find the trend-line of temperature decline (Figure D.2). After the oxygen was slowly released from the oxygen bomb, residual iron fuse wire was removed and weighed. The calorimeter was then cleaned and dried in preparation for the next experiment.

Equations and Statistics

The data logger information was exported from HOBOWare Pro to Microsoft Excel. The approximate temperature change was calculated from the corrected initial temperature (T_1), and corrected final temperature (T_2), from trend-lines extrapolated to half the detonation time. Thus, we find the corrected change in temperature, $T_2 - T_1 = \Delta T$.

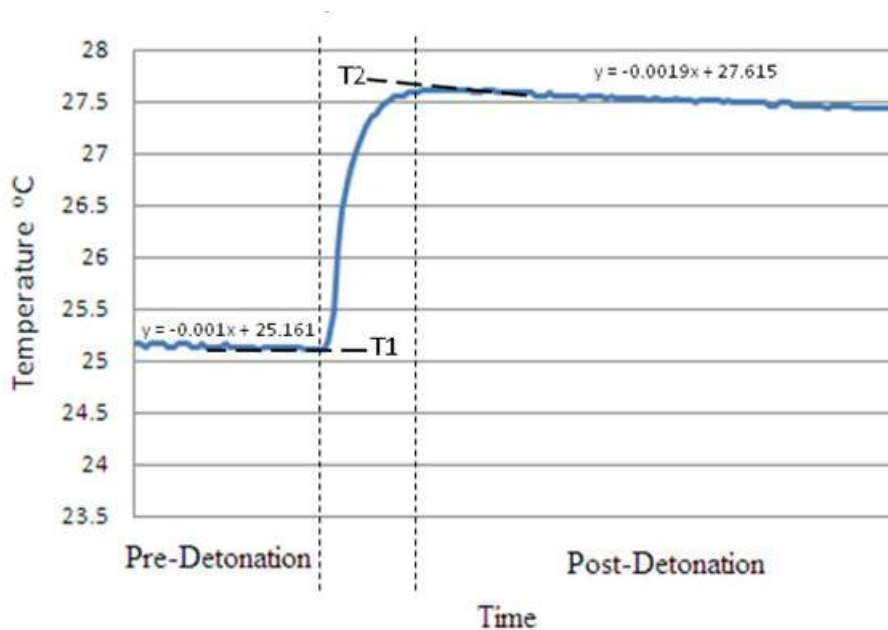


Figure D.2 Example of a graph of temperature over time, and trend-line equations.

To find the heat capacity (C_s) of the calorimeter the following equation was used:

$$\frac{\Delta E_t}{\Delta T} = \frac{\Delta E_{ba} * m_{ba} + \Delta E_{Fe} * m_{Fe}}{\Delta T} = C_s$$

Where m_b is the mass of the benzoic acid tablet and m_{Fe} is the mass of the iron fuse wire burned during combustion ($m_{Fe} = m_{Fe \text{ Initial}} - m_{Fe \text{ Residual}}$). An average heat capacity was calculated with multiple calibration experiments for both calorimeters. To calculate the energy released from a carabid beetle, the following equation was used:

$$\Delta E_{\text{sample}} = \frac{C_s * \Delta T - \Delta E_{Fe} * m_{Fe} - \Delta E_{\text{saran}} * m_{\text{saran}}}{m_{\text{sample}}}$$

Where m_{sample} is the mass of the beetle sample, and m_{saran} is the mass of the Saran Wrap used to wrap the beetle sample.

LITERATURE CITED

Schremph, H. 2001. Recognition and degradation of chitin by streptomycetes. *Antonie van Leeuwenhoek* **79**:285-289.